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Founded by J. A. Nieuwland, C.S.C.

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CONTENTS

The Life History of the Southern Spiny Lizard, Sceloporus undulatus undulatus Latreille ..... John W. Crenshaw, Jr. 257

Yearly Food Habits of the River Otter in the Thompson Lakes Region, Northwestern Montana, as Indicated by Scat Analyses ..... Kenneth R. Greer 299

Inter- and Intraspecific Variation in Oregon Frogs of the Genus Rana ..... Donald G. Dunlap 314

Food Habits of the Bullfrog in Central Missouri Farm Ponds ..... Leroy J. Korschgen and Don L. Moyle 332

The Population Dynamics of the Cliff Frog, Syrrhophus Marnocki ..... David L. Jameson 342

Correlation of Physiological and Behavior Indexes of Activity in the Study of Plethodon cinereus (Green) and Plethodon glutinosus (Green) ..... F. John Vernberg 382

Anatomy of Biomphalaria Boissyi as Related to its Infection with Schistosoma Mansoni ..... Emile T. Abdel-Malek 394

The Anatomy of the Gnathosoma of Pergamasus vargasi n. sp. (Acarina—Mesostigmata—Gamasides) ..... Flora E. Goritossi 405

A List of Cestode Parasites From California Mammals ..... Marietta Voge 413

Preliminary Aerial Survey of Microbiota in the Vicinity of Davenport, Iowa ..... James M. Vinje and Mary M. Vinje 418

Quantitative Distribution, Forest Soil Microorganisms in a Yellow Poplar Plantation ..... Robert D. Shipman 433

Pine Root Reaction in Sterile Culture to Mycorrhizal and Other Fungi ..... K. D. Doak 443

The Fossil Mosses of the Two Creeks Forest Bed of Wisconsin ..... William L. Culberson 452

Observations on Open-Grown, Non-Native Conifers in Southern Illinois ..... Leon S. Minckler 460

Vegetation of the Huachuca Mountains, Arizona ..... O. C. Wallmo 466

The Taxonomy of the North American Acaulescent White Violets ..... Norman H. Russell 481

Sugar Maple-Basswood Studies in the Forest-Prairie Transition of Central Missouri ..... C. L. Kucera and R. E. McDermott 495

Moorefield Woods: Old-Growth Beech in Switzerland County, Indiana ..... Howard E. Woodin 504

Notes and Discussion

A New Record for Cladophora Balls ..... Jesse F. Clovis 508

Notes on Arabis ..... Bernard Boivin 510

Additional South Dakota Terrestrial Gastropod Records ..... Ernest J. Roscoe 511

Vol. 54 October, 1955 No. 2

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The Life History of the Southern Spiny Lizard, Sceloporus undulatus undulatus Latreille[1]

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University of Missouri, Columbia

CONTENTS

Review of the literature	258	The nest	273
The study areas	260	Incubation period	274
Procedures	263	Egg size and development	275
Size, color and scutellation	265	Hatching and the hatchling	276
Life history	269	Growth	277
Eggs	269	Tail growth	291
Period of preoviposition development	271	Longevity	293
Time of oviposition	272	Summary	296

The present investigation was designed as a life history study of the southern spiny lizard, *Sceloporus undulatus undulatus* Latreille, in southwest Georgia, with emphasis on growth during the annual cycle. The populations of spiny lizards inhabiting two plots were selected for intensive study. While the bulk of the information was obtained from the study of the lizard populations in these selected plots, parallel and supplementary data were procured from occasional observation of lizards at various other localities in the general area.

A period of study at the Emory University Field Station, Baker County, Georgia, was made possible by an Emory University fellowship of the Robert Woodruff fund. Additional observations were made during a second period at the station while employed by the U. S. Public Health Service.

Acknowledgments.—For assistance in carrying out the present study I am indebted to Dr. Eugene P. Odum of the Department of Zoology, University of Georgia, who suggested and directed the study, for encouragement and assistance in many ways; to Major Melvin H. Goodwin, Jr., of the U. S. Public Health Service, Malaria Investigation Station, Newton, Georgia, for making the numerous appropriate arrangements in connection with both my periods of study at the Emory University Field Station; to Messrs. Milton Hopkins, James C. Major, Robert A. Norris, Hilary G. Parrish, George B. Rabb and George J. Schumacher, for considerable assistance in the field. Mr. Hopkins was especially helpful in assisting in last minute endeavors to obtain particular data and observations. For their many helpful suggestions, invaluable criticism and generous expenditure of time in editing this manuscript, I am grateful to Dr. Archie F. Carr, Mrs. Helen T. Gaige, Dr. Arnold B. Grobman, Dr. Albert M. Laessle, Dr. James A. Oliver, Dr. Karl P. Schmidt and Dr. Donald C. Scott. I wish to thank my wife, Nell Phillips Crenshaw, for constant encouragement and cheerful assistance in a multitude of ways. I have reserved for special mention Dr. R. E. Bellamy, until recently of the U. S. Public Heath Service Malaria Investigation Service, Newton, Georgia, who, although having no formal obli-

[1] Adapted from a thesis accepted by the University of Georgia in partial fulfillment of the requirements for the Master of Science degree. The research was carried out as part of a cooperative effort on the part of the University of Georgia and the Emory University Field Station and is published with the aid of a grant from the latter institution.

gation to assist in any manner, has contributed to the study in countless ways, both mental and manual, from the inception of the problem to the present.

REVIEW OF THE LITERATURE

Smith (1938), in reviewing the subspecies of *Sceloporus undulatus*, restricted the subspecific name *undulatus* to a largescaled race ranging from southeastern Louisiana through the basal half of the Florida peninsula to central South Carolina in the coastal area. Prior to his paper, the name *S. u. undulatus* also included the northern race for which Smith revived the name *fasciatus*. Subsequently the name *fasciatus* was found to be unavailable, and the name *hyacinthinus* was revived and used instead (Smith, 1948). Although earlier workers had recognized a southern race of *S. undulatus*, they failed to observe that specimens from Charleston, South Carolina, the type locality of *undulatus*, were identical with the specimens from other southern coastal areas. A type specimen is not in existence, since Latreille described this form from a description sent to him by Bosc.

Good studies on some phases of the life history of several species of the genus *Sceloporus* may be found in the literature. The Texan spiny lizard, *S. olivaceus* was the subject of an excellent field study by Newman and Patterson (1909). Emphasis was placed on modal habitat, reproduction and behavior responses to climate, enemies, food and water. Noble and Bradley (1933) and Noble (1934) reported on the territorial responses and courtship behavior of the northern spiny lizard, *S. u. hyacinthinus*. A very good general account of the life history and behavior of the same race was written by McClellan, Mansueti and Groves (1943). In the western United States, Fitch (1940) published a detailed study of the growth, courtship, territorial behavior and population replacement of the Pacific fence lizard, *S. o. occidentalis*. The territorial behavior, reproduction, growth, and longevity of the mountain swift, *S. graciosus gracilis*, have been studied by Stebbins and reported on in a series of papers (Stebbins, 1944, 1948; Stebbins and Robinson, 1946).

Wright and Funkhouser (1915) described in some detail the coloration, scutellation and general morphology of a series of specimens of the southern spiny lizard from the Okefenokee Swamp in southeastern Georgia. A brief account of the habitat of this race was also given. Barbour (1919) compared the distribution and habitat of this species with that of the Florida spiny lizard, *S. woodi*, in the State of Florida. Burt (1937) listed the types of situations in and about which *S. u. undulatus* has been observed. Burt's paper preceded Smith's clarification of the distribution of *undulatus* and *hyacinthinus* (1938) and had reference to both subspecies. Thus, although most of his listed habitats are equally applicable to both, a few seem to apply better to one or the other race. Although brief, the most complete account of the southern spiny lizard for a particular area is that given by Carr (1940) for the State of Florida. He adds to Barbour's earlier notes on distribution and habitat, and presents observations on food habits and reproduction. A summary of most of the above material, a distribution map, and photographs of this race are given by Smith (1946) in his Handbook of Lizards. There is not, however, a detailed life history study of the southern spiny lizard in the literature.

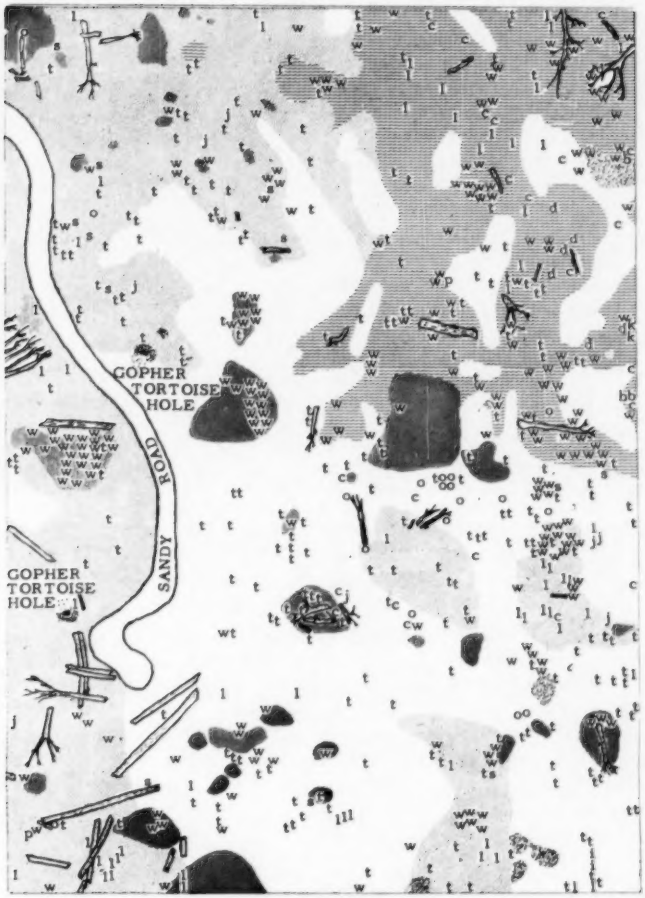

FIG. 1.—Map of Study Area 1, part of a scrub-oak forest in southwest Georgia.

FIG. 2.—A view of the scrub-oak forest of Study Area 1. Small trees in the foreground to left of center are turkey oaks. Clumps of wiregrass and bunch grass may be seen beneath the small oaks and in the background. To right of center is a clump of saw-palmetto. Photograph by M. H. Goodwin.

THE STUDY AREAS

Populations of the southern spiny lizard were studied in two different areas, both located in Baker County, Georgia. Area 1, a dry, scrub-oak forest, located in the southern part of the county, was studied intensively during the five month's period from the middle of April to the middle of September, 1948. Several trips were made to the area during the winter of 1948, and spring of 1949. Thereafter, it was visited infrequently until June, 1950, when departure from the general area necessitated interruption of the study.

Area 2, an incipient mesic-hammock forest, located in western Baker County, was visited less regularly but was studied intensively over a longer period of time than Area 1. Observations were begun in July, 1949, and were continued to the middle of May, 1950. This study area was selected in the light of what had been learned during the previous summer's work and is believed to approach more closely the optimum habitat, as judged by relative abundance, for the adult spiny lizard in this region.

Description of Study Area 1.—A rectangular section of sandy, scrub-oak forest,[2] 100 yards in length and 70 yards in width (roughly one and one-half acres in extent) was selected for the first area of study (fig. 1).

[2] In general, plant association nomenclature used here follows Laessle (1942), and variance from his terminology will be noted. The expression, scrub-oak forest, is such an exception and will be discussed subsequently.

The plot is located about twelve miles southwest of Newton, Baker County, Georgia, west of and immediately adjacent to the Ichauwaynochaway Creek.

In general aspect, the study area is gently sloping to level, well drained and quite open. Small oaks are scattered singly and in groups over the section while the few stands of large oaks and pines are widely spaced. Wire grass, the dominant ground story element, gives way at intervals to islands of oak seedlings and, rarely, saw-palmetto, and to small exposures of gray sandy soil (fig. 2).

Along its eastern boundary, the area is separated from the Ichauwaynochaway Creek by a dense mesic hammock which lies within a bend of the creek. Several gullies, from ten to fifteen feet in depth and running north and south, parallel the longitudinal axis of the scrub-oak area and are situated between it and the hammock.

To the west of the study area, the scrub-oak flora gradually diminishes and gives way to longleaf pineland. Both this and the scrub-oak forest mentioned above are included by Laessle (1942) in his "*Pinus australis* (= *palustris*) — *Quercus laevis* association." For the purposes of this study, it is convenient to separate this association into two facies. One of these is dominated by longleaf-pine (*Pinus palustris*) and often virtually lacks the turkey-oak (*Quercus laevis*). The other facies is dominated by turkey-oak and scrub white-oak (*Quercus stellata Margaretta*) and may be found with or without longleaf-pine. These two facies do intergrade commonly, but as a rule, either longleaf-pine or turkey-oak dominates. Some animals recognize differences in the conditions existing in these two subassociations and react accordingly. For example, the spiny lizard is uncommon in the longleaf pineland but is relatively abundant, especially during the winter months, in the scrub-oak forest.

The two species of scrub-oak, the scrub white-oak or post-oak and the turkey-oak, occur in equal numbers and are dominant throughout the greater part of the study area. Longleaf-pine (*Pinus palustris*) probably was at one time the dominant tree. While today this species is represented by small stands in the southwestern and northcentral sections of the area, the presence of numerous pine stumps attest to its greater abundance in the past.

Wiregrass (*Aristida stricta*) makes up the greater part of the understory and is present over most of the area. In the lower and better shaded regions, bunch-grasses (*Andropogon* sp.), bracken (*Pteridium aquilina*), and poison oak (*T. toxicodendron*) are scattered throughout the wiregrass. In more exposed situations, small patches of the sensitive-plant (*Cassia* sp.) are frequently encountered. Several clumps of the saw-palmetto (*Serenoa repens*) flourish along the eastern side of the area.

Description of Study Area 2.—The habitat selected for the second area, a deeply shaded incipient mesic hammock, is quite different from the open scrub-oak forest of the first area. The hammock study area (fig. 3), a curving strip about 140 yards long and 15 to 35 yards wide (slightly larger than half an acre), is situated at the southwest edge of Mossy Pond, a shallow, semipermanent, cypress-gum-buttonbush pond of limesink origin. It is located about 1¾ miles northeast of the junction of Baker, Miller, and Early counties. The area is almost level and usually well drained. Between

the essentially complete canopy formed by large trees, oaks for the most part, and the leaf littered forest floor, shrub and ground cover vegetation are very sparse imparting to the terrain a park like appearance (fig. 4).

Parallel to the hammock strip and some 75 yards to the southwest lies the floodplain of Big Cypress Creek, a semipermanent stream, which was quite dry during most of the period of study. Between the hammock and the floodplain there is an open scrub-oak forest dotted with an occasional long-

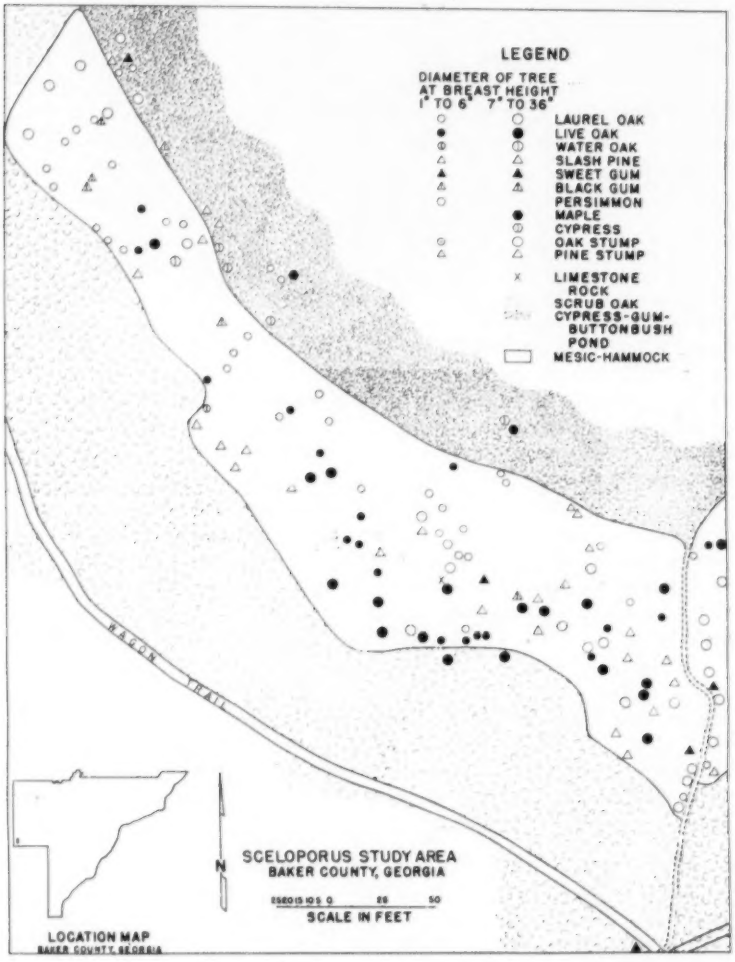

Fig. 3.—Map of Study Area 2 showing hammock and adjacent plant associations. Parallel broken lines crossing the eastern edge of the hammock from north to south represent a drainage ditch connecting the pond at upper right with Big Cypress Creek to the south of the area mapped.

FIG. 4.—View of hammock of Study Area 2, a habitat of the adult spiny lizard. The exposed roots of the large laurel-oak in the left foreground were often used as resting places by several adult females.

leaf-pine. Although generally similar to Study Area 1, this scrub-oak forest is more open. Numerous pine stumps scattered about indicate that the longleaf-pine may once have been rather common if not dominant over most of the area.

Along the northeastern or pondward side, the hammock study area is dominated by laurel-oak (*Quercus laurifolia*). In lesser numbers are splash-pine (*Pinus eliotii*), live-oak (*Quercus virginiana*), persimmon (*Diospyros virginiana*), sweet-gum (*Liquidamber Styraciflua*) and black-gum (*Nyssa sylvatica*).

The term hammock has been defined by Laessle (1942) as woods dominated by broadleaved evergreen trees. The climax vegetational association of the coastal plain in the southeast United States is a mesic hammock, typically dominated by magnolia (*Magnolia grandiflora*) and holly (*Ilex opaca*). In southwest Georgia, where there is a slight northern or piedmont floral influence, beech (*Fagus grandiflora*), although sometimes absent, usually occurs as a dominant in climax hammock associations (Thorne, 1948). While the study area hammock is more or less mesic in character, none of the mesic hammock dominants mentioned above is represented. The presence of such species as sweet-gum, black-gum and slash-pine, characteristic of hydric hammock, suggest a sub-climax stage in the hydrosere, not too far from hydric-hammock.

PROCEDURES

During April and May of 1948, Study Area 1 was visited six times, the greater part of the day being spent in the area at each visit. From June to

September the area was visited three times a week, each visit being of at least four hours' duration. These visits were arranged so that each week one would extend from 6:00 to 10:00 a.m., another from 10:00 a.m. to 2:00 p.m. and the other from 1:00 to 5:00 p.m. Other trips were made to the area as time permitted. This system was followed with few exceptions until the conclusion of the summer's work. As much time was spent in the area on subsequent visits as was possible.

During the 44 weeks of investigation in Study Area 2, it was visited 52 times. These visits varied from two to eight hours in length, averaging about four hours. One interval slightly in excess of three weeks and two intervals about two weeks each elapsed between visits to the area. On the other hand, the area was visited daily for as many as three consecutive days. More time was spent in the area in afternoons than in mornings although arrival at the area was, on several occasions, as early as 6:30 a.m. and departure as late as 8:15 p.m.

The usual procedure for locating lizards in both areas was to move slowly back and forth across the study plot observing all tree trunks, rocks and the terrain in general.

The method used in capturing a lizard varied with the circumstances, but was usually some modification of the familiar "grab as grab can" technique. The noose was resorted to only when the lizard sought was out of reach of the hand. Usually a lizard, after being taken by the noose, would remain suspicious of its presence for several weeks.

At initial capture, lizards were permanently marked by clipping toes in different combinations according to the method used by Fitch (1940) and Stebbins (1944). This type of mark was employed in preference to metal tags, clipped scales, or daubs of indelible paint because of its simplicity and permanence. In Study Area 2 lizards were also marked with india ink spots or stripes in order both to facilitate recognition and to obtain data on the frequency of molting. Such markings, also employed by Noble (1934) and Fitch (1940), remain only until a lizard molts. Thus, if a recaptured lizard still has its ink mark it is known not to have molted since its previous capture, and a lizard found to have lost its mark is known to have shed its skin one or more times. In addition to the toe identification formula and ink mark, the sex, dorsal scale count, general body color and abnormalities were recorded at initial capture. Data recorded at the first and at subsequent captures were: date, time of day, exact location, snout-vent and usually tail length, and, occasionally, weight. Notations were also made with regard to behavior, resting place, and breeding condition.

Age group designations used in this study are defined as follows: hatchling—a lizard bearing an umbilical scar and usually from 21 to 26 mm in snout-vent length; juvenile—a lizard that has lost the umbilical scar and is 51 mm or less in snout-vent length; young adult—a lizard having a snout-vent length of from 51.5 to 58 mm (the smallest lizard found to contain oviducal eggs was 52 mm in snout-vent length); adult—a lizard having a snout-vent length of more than 58 mm.

In Study Area 1, from April 7 to September 5, 1948, a total of 74 lizards were marked. Eighteen of these, 6 males and 12 females, were

adult or young adult. Of the remaining 56 juveniles and hatchlings, 33 were sexed. Eighteen proved to be males, 15 were females.

In Study Area 2, 56 lizards were marked from July 6, 1949 to May 10, 1950. Thirty-four of these, 17 males and 17 females, were adult or young adult. Of the remaining 22, all juveniles, there were 16 males and 6 females.

SIZE, COLOR, AND SCUTELLATION

Of 335 lizards measured, the longest, a male, was 168.5 mm in length; of this the snout-vent length was 65.5 mm, the tail 103 mm. The longest female measured was 165 mm over-all with a 70 mm head and body and a 95 mm tail. The female appears to attain a greater head-body length than the male. The four greatest snout-vent lengths found for females were 69, 69.5, 70, and 70 mm; the four corresponding male snout-vent lengths were 65.5, 65.5, 66, and 66 mm. In old adult lizards, the tail of the male appears to be longer than that of the female. For example, in males the four longest tails measured were 98.5, 100, 103, and 103 mm, as compared with greatest tail lengths of 92, 92.5, 95 and 97 mm for females. This sexual dimorphism in relative tail lengths is not found in juvenile or young adult lizards.

There are not sufficient measurements of lizards of this race from other areas to compare satisfactorily the maximum size attained in various populations. Snout-vent lengths of 77 mm and 72 mm are reported for a male and female respectively as the largest of several hundred southern spiny lizards measured (Smith, 1946). Locality data are not given for these exceptionally large specimens. The largest individual of a series collected in the Okefenokee Swamp of southeastern Georgia was somewhat smaller than those from this area, measuring 155 mm in total length (Wright and Funkhouser, 1915). However, the series examined is too small to permit significant comparison. A series of ten specimens from the Shubuta, Mississippi area, purchased from a commercial concern, contained one male with a greater head-body length (67.5 mm) than the largest male examined from the southwest Georgia area.

Although the southern race is said to be a little larger on the whole than the northern subspecies, *S. u. hyacinthinus*, (Smith, 1946), specimens from the area studied appear to have lesser body dimensions. Smith gives snout-vent lengths of 72 mm for a male and 79 mm for a female as the largest of several hundred specimens of the northern race measured. A large adult male and female of the same race from Maryland had snout-vent lengths of 69.5 and 76.5 mm respectively (McClellan, Mansueti and Groves, 1943). Maximum body lengths of examples of the southern race from southwest Georgia fall considerably short of these measurements.

The markings of this form have been described in some detail (Smith, 1946; Wright and Funkhouser, 1915). In life the dorsal ground color of the male varies from dark gray or black to light brown. A broad band, usually darker than the dorsal ground color, extends from axilla to groin along the sides of the body. A series of 7 or 8 wavy, brown to black bars, frequently broken or incomplete, traverse the body dorsally from side to side. These bars are continued posteriorly as dark rings encircling the tail. Dark bands are usually present on the forelegs and hind legs, extending as rings

onto the digits. The dorsal cross-bars of the male sometimes are of a bright bronze hue. This "bronze-back" condition is more or less characteristic of certain specimens, but was observed in most adult males at certain times, notably during the breeding season.

Ventrally, paired lateral blotches of a dark green to deep blue color extend between the forelimb and hind limb. Paired blotches of similar color are present in the gular region; these may join to form a single large band

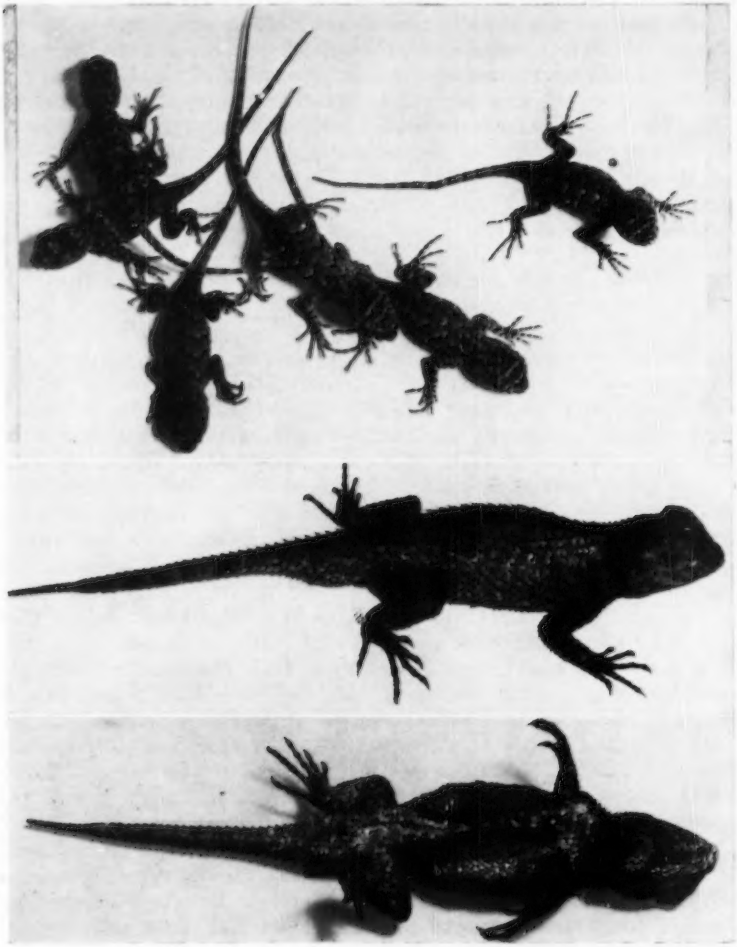

FIG. 5.—Upper: Hatchling spiny lizards several days after emergence from the egg. Photograph by M. H. Goodwin. Center and lower: A large male spiny lizard showing a pronounced tendency to melanism. Courtesy U. S. Public Health Service.

extending across the throat. Both belly and throat patches are bordered with black. In young adult males these black borders are narrow so that light areas are present between and anterior to the gular blotches on the throat, between the forearms and extending posteriorly between the lateral belly blotches to a broad, light subpelvic area. As the lizard grows, the black borders of the gular and belly blotches broaden and merge midventrally both on the throat and abdomen. Thus, in a very old male, the anterior portion of the lower jaws, a narrow subpectoral, and a slightly larger sub-pelvic area are the only light ventral areas remaining.

The color pattern of the female is somewhat similar to that of the male. Dorsal markings are generally dull gray or brown, and the crossbars are usually more clearly defined than on the male. These bars vary from dark gray or brown to black and generally are visible on the sides through the lateral bands. Ventrally, paired gular and belly blotches are usually present but may be completely lacking. These blotches are lighter in hue than those of the male, and range from very pale green to deep blue. Gular and belly patches may have partial black borders but usually have none. Only one female or more than a hundred examined was found to have ventral blotches completely bordered by black as is characteristic of the adult male. This tendency toward the development of partial black borders in females is often associated with large size. Light areas about the ventral blotches, or the entire ventral surface when blotches are lacking, are white speckled with black or, rarely, immaculate white. Black speckles in the mid-ventral region tend to coalesce to form a longitudinal line in both males and females, but this tendency is especially noticeable in the latter.

Markings of hatchling males and females are identical (fig. 5), approaching very closely those of the adult female. Neither gular nor belly blotches are present.

Melanistic tendencies have been reported in examples of this race from southeast Georgia (Wright and Funkhouser, 1915). Unusually heavily pigmented individuals were observed from time to time during the present study. Such melanism was observed to be of at least three types. The most commonly noted type was a temporary darkening presumably brought about by certain environmental conditions. Environmental factors that control color change in lizards have been summarized by Smith (1946) as: temperature, state of excitation, health or physical state and light. Only the first of these factors, temperature, was observed to be closely correlated with appreciable darkening in the southern spiny lizard. A majority of the lizards observed on cool, sunny days were quite dark, regardless of sex, age or color of substrate. Some specimens, usually quite clearly marked, became a uniform dull gray or black dorsally during such periods; ventral surfaces were not appreciably obscured. Such increase in pigmentation on cool sunny days may be of considerable value in facilitating the absorption of heat.

Light, or color of substrate, probably also affect to some extent the darkness of the spiny lizard, but available data are not sufficient to indicate this. Moisture is not listed by Smith as one of the factors controlling color change, but it was evident that most lizards taken during rainy periods or in moist situations were quite dark. This condition may be entirely the result of a moist or wet skin, which does make the lizard appear darker,

but it may well result in part also from a melanophore effect stimulated by moist conditions.

A second variety of melanism noted was that of general darkening associated with old age. Apparently this effect rarely produced a uniform dark gray or black dorsum. The enlarging of ventral dark areas with age has been mentioned above.

The third and most extreme type of melanism observed was that found to be characteristic of a few individuals (fig. 5). This condition is probably genetically controlled. In these specimens, dorsal shades of darkness were found to range from dark grays with faintly visible patterns to uniform sooty or lustrous blacks. In individual lizards these shades varied within narrow limits both seasonally and with advancing years. Probably such melanism is developed shortly before attainment of maturity and appears to be restricted to a very small proportion of the lizards in a population. In both males and females exhibiting this condition, an unusually large amount of dark pigment was present on ventral surfaces. The black borders of belly and gular blotches in males are more extensive and, in females, a gray suffusion may replace ventral light areas.

The arrangement of head scales of the southern spiny lizard has been diagrammed by Cope (1900) and Wright and Funkhouser (1915). Smith (1938) has presented a table of comparison of the body scale counts (dorsal scale count, number of scales around the body, number of femoral pores and number of scales between femoral pore series) of the seven subspecies of *S. undulatus*. The southern race was found to have the lowest dorsal scale count (31 to 40) of any of these races. The northeastern subspecies was found to have dorsal scale counts of from 35 to 49. Although other differences are known between these two races, *hyacinthinus* and *undulatus*, only the scale count difference is of practical value in distinguishing the two forms. Since there is considerable overlap in dorsal scale count, Smith (1938) selected 37, the count at which he found the least overlap, as the intermediate point between the two races. Thus, if the average number of dorsal scales of a series from a particular locality is 37 or less, the specimens can be referred to the southern race.

Evidence at hand indicates that the area of intergradation between *undulatus* and *hyacinthinus* is quite broad in the State of Georgia and suggests that the north to south reduction in dorsal scale count may form a cline. The fact that Smith found a scale count at which there was appreciably less overlap than elsewhere would not be compatible with a clinal change if the entire ranges of the two subspecies had been adequately sampled. However, Smith's distribution map (1938) suggests that the area at which one would expect the greatest number of dorsal scale counts of 37, *i.e.*, the area of intergradation, is very poorly represented.

Dorsal scale counts were made on 191 spiny lizards from three populations located roughly 85 miles south of the fall line in southwest Georgia (table 1 and fig. 6). The three populations, designated A, B, and C, are separated from one another by permanent streams, the Ichauwaynochaway Creek and Flint River. Examination of the dorsal scale counts of these three populations, treating males and females separately, reveals that the mean dorsal scale count is highest in population A, lowest in population C

and intermediate in population B. When subjected to statistical analysis, the difference in the mean dorsal scale count of males from populations A and C was found to be highly significant (t value = 3.14). Mean differences between males of populations A and B, and B and C did not reach the .01 level of significance. Differences in mean dorsal scale count between females of populations A and B, B and C, and A and C also failed to reach this level. However, the examination of larger samples of females, especially from populations B and C, than are available at this time may help in the evaluation of this significance.

A west to east reduction in dorsal scale count, which probably reflects a northwest to southeast reduction, would be expected in the area studied if there is a clinal reduction in scale count from the piedmont of Georgia through the coastal plain toward peninsular Florida. Population A is about 100 miles south of the piedmont and *hyacinthinus* populations. Population B is about the same distance south of the fall line, but it is separated by one less permanent water barrier from peninsular Florida. In turn, population C is another step (or water barrier) closer to peninsular Florida. The above evidence, indicating a reduction in dorsal scale count from populations northwest of the Flint River to populations southeast thereof, would be consistent with a clinal reduction in scale count from north Georgia *hyacinthinus* populations to peninsular Florida populations of *undulatus*. Available evidence is no more indicative of sub-specific relationship than of continual north-south clinal variation in the populations of *S. undulatus* of the eastern United States.

In each of the populations discussed above, it was observed that the mean dorsal scale count of females was higher than that of males. In populations A and C, these differences were not significant (t value = 1.39 and 1.76 respectively), but in population B the difference in mean scale count of males and females was highly significant (t value = 3.28).

LIFE HISTORY

EGGS

In Florida clutches of "nine to thirteen eggs are laid (by the southern spiny lizard) in April and May under old logs and in beetle frass" (Carr, 1940). In southwest Georgia the number of eggs deposited appears to be

TABLE I.—Dorsal scale count variation of *Sceloporus u. undulatus* in southwest Georgia.

Population		Number Examined	Scale Count Range	Mean Scale Count
A—West of Ichauwaynochaway Creek				
	males	56	29-37	33.27 ± .22
	females	62	30-38	33.69 ± .21
B—Between Ichauwaynochaway Creek and Flint River				
	males	17	31-36	32.29 ± .31
	females	18	31-36	33.67 ± .26
C—East of Flint River....				
	males	25	28-36	31.92 ± .34
	females	13	31-36	33.00 ± .51

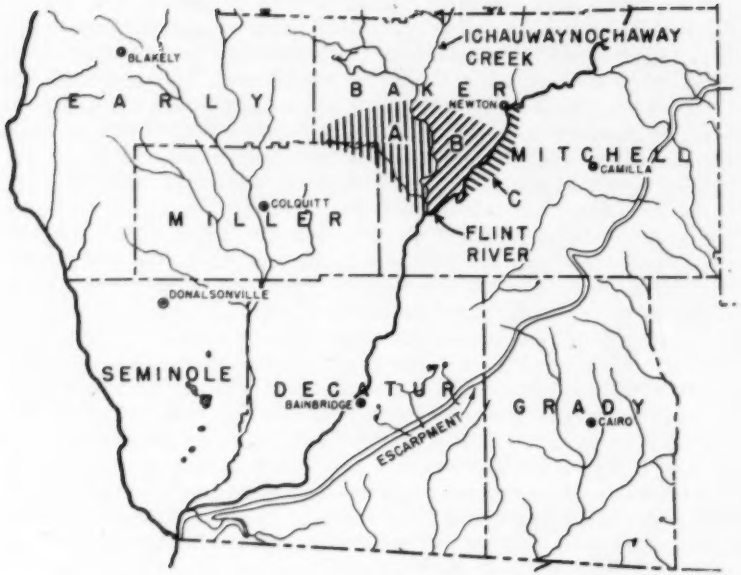

Fig. 6.—Location of spiny lizard populations from which dorsal scale counts, shown in table 1, were obtained.

somewhat smaller. Of eleven clutches laid in captivity, the average number of eggs was 7.6 with extremes of 6 to 10. Very young gravid females were not found to contain more than six or seven eggs. Large females generally deposited larger clutches, although clutch size was not closely correlated with size of the parent female. A clutch of 10 eggs was deposited by a lizard having a snout-vent length of 66 mm., whereas clutches of 8 eggs were laid by females having snout-vent lengths of 60 mm., 65 mm., and 70 mm.

Several females apparently were able to delay egg deposition until favorable nesting sites were found. Others would deposit their entire complement in situations most unfavorable for proper incubation. One specimen in such a situation, perhaps unable to postpone oviposition longer, deposited a single egg on the bare floor of her cage. Another was deposited on the following day before the lizard was removed to a cage containing more favorable nesting sites.

The eggs are fairly uniform in shape, being elongate-oval and, in cross-section, sub-circular (fig. 7). At deposition the egg is usually slightly asymmetrical. The outer integument is thin and translucent, and the embryo disk is faintly visible through the shell. As time passes the shell thickens, loses its translucence and becomes an immaculate white. Although apparently smooth, close examination discloses the presence of fine elongate pits and striations in the outer integument. Size and growth of the egg are discussed below under Incubation Period.

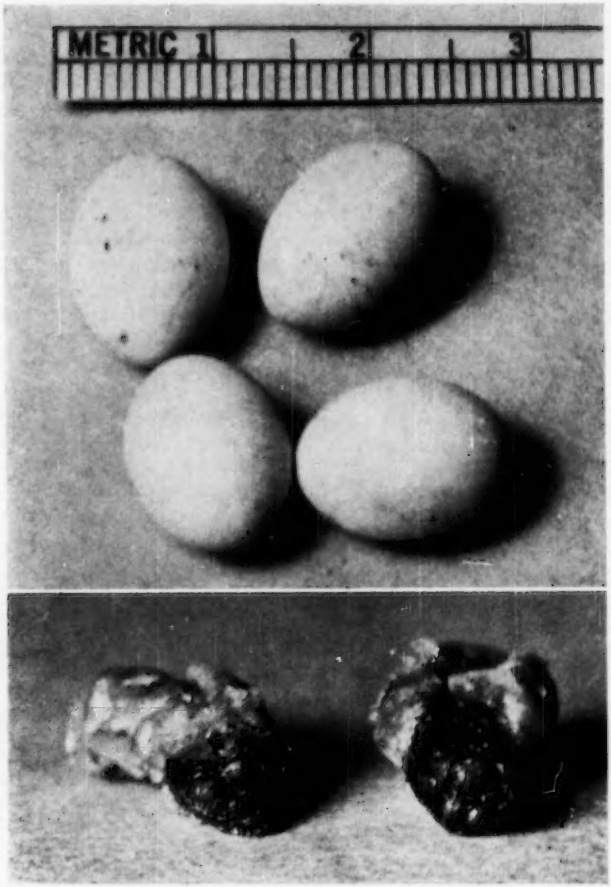

Fig. 7.—Upper: Eggs of the spiny lizard about two weeks prior to hatching. Lower: Young spiny lizards hatching. Particles clinging to collapsed egg shells are grains of sand.

PERIOD OF PREOVIPOSITION DEVELOPMENT

Data compiled during the present study concerning the length of the preoviposition developmental period of eggs of the spiny lizard are unfortunately far from conclusive. Since but little is known regarding this period in most lizards, pertinent observations are presented here for what they may be worth. Five gravid females of the spiny lizard, isolated from males after capture, deposited their eggs 4, 13, 22, 24 and 27 days following collection. In each of these cases the female was captured several weeks subsequent to the beginning of courtship activity in the general area. Six females, all taken on the same day but not isolated from males, deposited fertile eggs 21, 30, 34, 34, 35 and 41 days after capture. These specimens were

captured early in the year, and, since oviposition dates tended to fall into groups, an attempt was made to correlate these dates of egg deposition with earlier climatic conditions which might have stimulated courtship. Suggestive relationships were found. The first warm spell of the spring began 39 days before the first oviposition date on May 2. During this first warm period, which lasted from March 24 through March 28, maximum daytime temperatures approached or exceeded 80° F. Minimum temperatures ranged from 42 to 59° F. The earliest courtship activity in the area was observed during this same warm period. In late January and early February temperatures remained high for several successive days, but, although over 75 spiny lizards were observed or captured, no pairing or courtship activity was noted. Such unseasonable warm spells of several days to a few weeks duration are not of unusual occurrence during the winter months in the general region. On April 2, temperatures rose for a second time and continued high through April 4. Maximum daily temperatures ranged from 75 to 84° F.; minimum recordings varied between 46 and 62° F. On May 11, 39 days after the beginning of this warm period, another lizard oviposited. Two lizards oviposited on May 15 and one on May 16, 41 and 42 days respectively following the last day of this second warm spell of the year. The remaining lizard deposited her egg complement on May 22, 41 days subsequent to capture and 43 days after the beginning of a third series of warm days lasting from April 9 through April 13. Maximum daily temperatures during this period ranged from 74 to 81° F., minimum temperatures from 40 to 49° F.

The five females that were isolated at capture (see above) also were found to have deposited their eggs between 39 and 41 days following one of the above or a later period of high temperatures.

It would appear, then, that the preoviposition developmental period of eggs of the spiny lizard in southwest Georgia lies somewhere between 27 and 43 days in length, probably very close to the latter figure. By comparison, a period of 7 to 8 weeks was found for a captive female of the northern spiny lizard (McClellan, Mansueti and Groves, 1943).

TIME OF OVIPOSITION

Carr (1940) reports that in Florida eggs of the spiny lizard are laid in April and May. For the northern race in Maryland, oviposition dates ranging from May 27 to June 12 are reported (McClellan, Mansueti and Groves, 1943). Several dates of egg deposition have been given above for southwest Georgia. One of these, May 2, 1950, is the earliest noted by me. Other observations for the same month and year were made on the 11th (2 clutches), 15th (2 clutches), 16th, 20th, 22nd and the 24th. Since there apparently is a relationship between time of oviposition and early warm periods, (i.e. late winter or early spring) dates of oviposition should not be considered as "times of the year" at which egg deposition takes place for a particular species but rather as oviposition times for a given year and geographical location.

Observations in Study Area 2 during the late summer and fall of 1949 provide further information as to the extent of the egg deposition period. Early oviposition was indicated by the presence of juveniles in the area by

mid-July. By examining adult female lizards at each capture for contained eggs, it was possible to obtain dates bracketing egg deposition. For three lizards thus examined oviposition was found to have occurred between July 19 and July 25, July 19 and August 18, and July 25 and August 12. Another lizard examined and found gravid on July 25 was not recaptured. Probably oviposition occurs only rarely after late July or early August in most years.

The three months' period during which eggs are laid suggests that more than a single clutch may be deposited by a given lizard in a season. This was not conclusively demonstrated though such a possibility was supported by other observations. More than three clutches would not be possible in a May to August egg-laying period, and even this number would require an early first breeding and a rapid succession of preoviposition developmental periods. For lizards depositing their first clutch after the middle of May (and this would include a good majority) a maximum of two clutches would seem more probable.

Three adult females, collected and preserved shortly after egg laying season, were found to contain from 21 to 25 ovarian follicles, all quite small and graded in size from something less than 0.5 mm to about 2.0 mm in greatest diameter. An adult female preserved early in the egg laying season, but before she had deposited her first clutch, was found to contain eight well developed ova, ranging from about 5.5 mm to 6.5 mm in greatest diameter, in addition to ten small ovarian follicles from 0.5 mm to 1.5 mm in diameter. Another female preserved toward the end of the oviposition period on July 24, contained seven large ova between 7.5 mm and 8.5 mm in greatest diameter, presumably her second clutch of the season. Also found were six small ovarian follicles between 0.5 mm and 1.5 mm in diameter. The decrease in the number of small ovarian follicles as the oviposition season progresses suggests that the supply may be depleted by more than a single clutch of eggs.

THE NEST

Although considerable time was spent in searching for nests of the spiny lizard in areas known to sustain large populations, none was found. Four clutches of eggs deposited in the laboratory, in containers offering a variety of conditions, may provide some idea as to modal nest-site in the wild. The bottom of a large, rectangular aquarium was covered with two to three inches of sand. Into this sand, at one end of the aquarium, a fingerbowl, filled with sand and water, was sunk to just over its brim. Water seeping out over the rim of the fingerbowl kept one end of the aquarium slightly moist leaving the other quite dry. A split oak limb, about four inches in diameter, was placed, flat surface down, along one side of the aquarium in such a way that it covered areas of both moist and dry sand. A mat of dried Spanish "Moss" was placed along the other side of the aquarium, also extending over moist and dry areas. One of several gravid females placed in this aquarium deposited eight eggs. These were found in a group at the bottom of the fingerbowl covered by about one and a half inches of wet sand. Enough water had escaped from the bowl so that the sand was no longer saturated.

A cage was also prepared that offered nesting situations nearly identical to those of the aquarium. Instead of using a fingerbowl as a source of moisture, a water filled jar having a minute hole in its cap was inverted in the sand. Three females deposited eggs in this cage. Two lizards oviposited in moist spots adjacent to the water-containing jar in open sand. One of these deposited its ten eggs in a group under about 1.5 inches of sand. The other deposited four eggs together under 2 inches of sand and, a day later, two more at the surface. The third lizard deposited her clutch in a moist spot beneath the split limb. Two eggs were found under an inch of sand; four others rested between the limb and the surface on moist sand which was brought up by the lizard in digging a nest for the first two eggs. In these, and in several other instances in the laboratory, female spiny lizards have always deposited their eggs in sand, when available. They have also consistently utilized moist areas when possible. None of the females in the laboratory has indicated any interest in her nest following oviposition.

Lizards were observed in the laboratory on two occasions as they excavated their nests. These worked after the manner described by Newman and Patterson (1909) for the Texan spiny lizard, using the forelimbs to dig and the hind limbs to move loose sand away from the excavation.

Egg deposition was not restricted to any particular period of the day. One clutch was deposited between 8:00 p.m. and 8:00 a.m. the following morning, probably during the early morning. Another clutch was deposited between 12:30 and 3:00 p.m. of the same day, and another between 10:00 a.m. and 2:30 p.m. A fourth clutch was deposited between 5:00 p.m. and 8:30 a.m. the next day. Judging from the appearance of the eggs, the latter clutch was probably deposited shortly after 5:00 p.m. Actual laying was not observed.

INCUBATION PERIOD

Three clutches of eggs deposited a short time after capture of the parent were retained in the laboratory until hatching. These were kept in an "incubator" consisting of one large and two slightly smaller fingerbowls. One of the small fingerbowls was half filled with moist sand on which the eggs were placed. This fingerbowl was stacked on the larger one which had been partially filled with water. A strip of paper towel extended from the water in the lower to the sand in the upper bowl. The remaining small fingerbowl was inverted and placed upon the bowl containing sand. The paper towel strip, by capillary action, served to keep the sand moist and the atmosphere in the "incubation" chamber humid. Eggs were kept in the laboratory, away from direct sunlight, at temperatures closely approximating those outside the building.

One clutch of seven eggs deposited between 10:00 a.m. and 2:30 p.m., June 29, 1949, began hatching about 5:00 p.m., August 25. At this time a single egg had been slit by the young spiny lizard within. Eggs continued to hatch during the night and following day until 5:00 p.m. when all young had emerged. The incubation periods of eggs in this clutch, then, varied from 57 to slightly over 58 days.

Another clutch of six eggs was deposited July 13, 1948. Hatching

began 49 days later, on August 31, and was completed by the afternoon of September 1.

Probably these periods of incubation found in the laboratory fall somewhere between the extremes in nature. Since environmental conditions in nature are so inconstant and unpredictable, the incubation period of eggs of the spiny lizard in natural habitats is certainly quite variable.

A large female, under observation for several months in Study Area 2 and known to be gravid, deposited her eggs between July 19 and July 25, 1949. On October 13, two juvenile lizards about one month old were taken within the home range of the female. Since no other gravid females had been observed near this portion of the study area, there is a strong possibility that these were the young of the female mentioned. It seems legitimate to infer that the incubation of these eggs required between 48 and 54 days, a period comparable with that in the laboratory.

For the northern spiny lizard in Maryland, laboratory incubation periods of 92 and 96 days (over one and one-half times as long as those found for the southern race) have been reported (McClellan, Mansueti and Groves, 1943). A clutch of eggs deposited by a female of the southern race on May 11, 1950, in southwest Georgia, and moved to Atlanta, Georgia, on June 1, hatched on July 28 after an incubation period of 78 days. There seems to be a general increase in length of incubation period as one moves from south to north, probably correlated with the decreasing mean temperatures.

Some eggs were lost during laboratory incubation as a result of fungus infestation; a few were lost presumably from lack of moisture. Usually all the eggs in the same container were similarly affected by detrimental factors. On one occasion, the early removal of an egg that had been attacked by a fungus saved the remainder of the complement. A single clutch was lost when too much water was inadvertently added to the sand in an incubator.

EGG SIZE AND DEVELOPMENT

Eggs of the spiny lizard vary but slightly in size within a single clutch. In different clutches at equivalent stages of development, size variation is somewhat greater and, with eggs of different ages, there is considerable difference both in size and shape. A clutch of seven freshly laid eggs, the largest measured, were found to vary from 14.0 to 15.0 mm in length (average 14.4 mm) and from 7.3 to 8.3 mm in width (average 7.7 mm). One of these, measuring 15.0 mm by 8.3 mm, was the largest freshly deposited egg observed. Another clutch composed of six eggs (which were the smallest measured) varied in length from 12.0 to 13.0 mm (average 12.5 mm) and from 6.5 to 8.0 mm in width (average 7.16 mm). The smallest egg measured, 12.0 mm by 6.5 mm, was one of this clutch.

Eggs of this lizard in Florida are reported to vary in size from 11.2 to 11.7 mm. by 6.5 to 7.1 mm. (Carr, 1940). Dr. Carr has informed me that these measurements were taken from eggs dissected out of gravid females, which fact probably accounts for their small size.

The clutch of seven eggs mentioned above as the largest observed was measured a few hours after oviposition and again the day hatching began. These eggs at deposition averaged 14.4 mm in length. Immediately before hatching began, 59 days later, these same eggs were found to average 18.6

mm in length, ranging from 17 to 20.5 mm. Thus they had increased in average length by 4.2 mm or 29 per cent. The relative increase in width had been even greater since eggs tend to become more spherical with incubation. This is indicated by the progress of a clutch of six eggs, the smallest measured. At deposition these averaged 12.5 mm in length and 7.16 mm in width. Ten days after deposition, length measurements varied from 13.0 to 14.0 mm, averaged 13.5 mm; width measurements ranged from 8.0 to 8.5 mm and averaged 8.16 mm. Thus, while increasing in average length 1.0 mm or 8 per cent, they had increased in width also by 1.0 mm but by 14 per cent. Forty-seven days after the eggs were laid they averaged 14.9 mm in length and ranged from 14.5 to 16.0 mm. The average width was 10.4 mm with extremes of 10.0 and 11.0 mm. At this time they had increased in average length by 19 per cent (2.4 mm) while expanding in width by 45 per cent (3.24 mm).

HATCHING AND THE HATCHLING

The hatchling spiny lizard is practically a duplicate in miniature of the adult female (fig. 5). The tail is relatively shorter, the head proportionately larger, and there is none of the blue or green color usually found laterally along the belly and in the throat region of the adult.

In every case thus far observed, the eggs of a single clutch have hatched and the young emerged within a 24-hour period. In one group of four eggs, 10 hours elapsed from the first appearance of a slit in an egg to the successful emergence of the last hatchling.

On July 28, at 7:00 p.m., a slit was observed in one of a clutch of eggs which had been under close observation since 3:00 p.m. The slit had not been present at a 6:00 p.m. examination. At 7:30 p.m. the snout tip of the young lizard was just beginning to protrude through the opening in the integument of the egg. At 8:25 p.m., the head and neck were forced rather abruptly through the slit (fig. 7). For over two hours thereafter, the lizard made no attempt to complete its exit from the egg. At 10:50 p.m. it was observed that the left forelimb was out, and, by 11:05 p.m., the other forelimb had emerged and the hind legs and tail only remained within the egg. For the next hour no further progress was made, but, shortly thereafter, a series of struggles freed both hind limbs and the tail. At this point, 12:25 a.m., only the umbilical cord attached to the collapsed egg barred the hatchling's way to complete freedom. At 12:40 a.m., roughly six hours after the hatching process began, the umbilical cord was broken and the process completed.

Hatchlings from a single clutch of eggs vary but slightly in size and proportion. As was found with eggs, variation between individuals of different clutches is somewhat greater. The largest hatchling lizard observed was 61.5 mm in overall length. Of this, the head and body accounted for 26.0 mm or about 42 per cent of the total length. The 35.5 mm tail was disproportionately long for a newly hatched lizard. The smallest newly hatched lizard examined measured 38.5 mm from snout to tail tip. The 20.5 mm snout-vent length comprised about 53 per cent of the total length, the 18.0 mm tail about 47 per cent.

The six siblings of the large (61.5 mm) hatchling mentioned above were

all relatively large. In overall length they ranged upward from 55.5 mm, averaging 58.9 mm. The tail of each of these was slightly longer than the head and body. The smallest lizard encountered (38.5 mm) and its three siblings averaged 42.1 mm in overall length and ranged upward to 43.5 mm. The tails of two of these were shorter than the snout-vent lengths. In all other lizards observed, adult or young, in which the tail had not been broken, this appendage was longer than the head and body.

Since the tail of the spiny lizard is so frequently broken, only the head-body, or snout-vent, length has been used in determining growth rate. Thus, the head-body length measurement has been recorded more often in field work than the tail or overall length. No juvenile observed in the field has had as short a snout-vent length as that of 20.5 mm recorded for the smallest laboratory hatchling, though lizards of this size almost certainly do occur in nature. There were recorded in the field two 22.0 mm head-body lengths and many of less than 26.5 mm, the maximum snout-vent length for a laboratory hatchling. Probably only a very small proportion of newly hatched lizards exceeds this maximum.

Six juveniles of a brood hatching on August 31, 1948, were weighed the following day. The hatchlings varied in snout-vent length from 21.0 to 23.0 mm, averaging 21.9 mm. Weights ranged from .40 to .45 g., averaging .428 g. Weights observed in the field, of recently hatched lizards having snout-vent lengths of 24.5 mm, 25.0 mm and 26.0 mm were respectively .55 g., .50 g. and 70 g.

Shortly after the umbilical cord has been broken, the portion attached to the lizard shrinks to form a small fleshy knot, closely applied to the abdominal surface. Within a day, the knot has disappeared, but a longitudinal midventral scar is clearly evident. Four days after hatching the umbilical scar has narrowed to a thin line of flesh, barely discernible between the midventral scale rows.

No malformation of any sort was observed among juveniles hatched in the laboratory, and only mutilations of the type resulting from predatory action or conflict were observed in the field.

The time of appearance of the first hatchling will, of course, vary from year to year and from one locality to another. In the summer of 1948, the first hatchling was taken on June 21 near Study Area 1. Until July 15, only five others had been collected, but by the end of July an additional 16 had been taken. Hatchling lizards continued to appear in numbers until the latter half of August after which only infrequent trips of short duration were made to the area. On September 5, a hatchling that could not have been more than a few hours old was taken. Unquestionably, some eggs hatched even after this date.

In Study Area 2, observations in the late summer of 1949 indicated that some hatchings had emerged from the nest about the middle of September. Two juveniles taken on October 13 were estimated to be about one month old and another, collected on November 4, could have been little more than a month out of egg.

GROWTH

The rate of growth of the spiny lizard during the warmer months of the year differs considerably from that observed during the cold months. Accord-

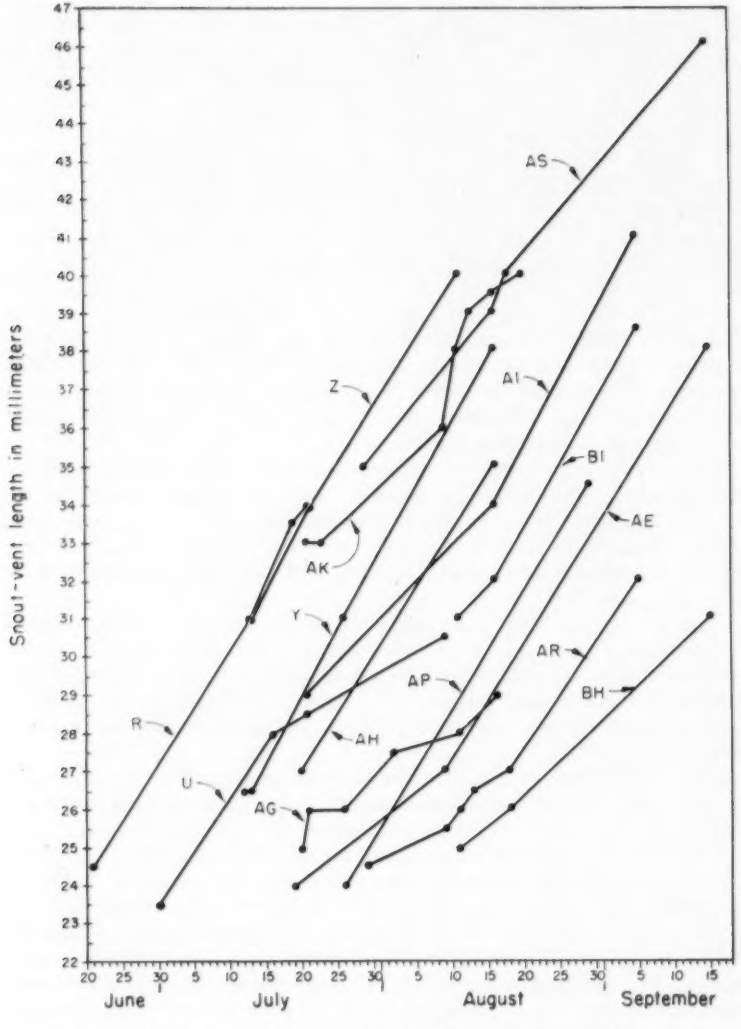

FIG. 8.—Increase in snout-vent length of the juvenile spiny lizard during the first growth period.

ingly, warm season and cold season growth have been treated separately for each yearly age group. The first warm season, in the sense the expression is used below, is the period of time between hatching and the beginning of cold weather that ushers in the first cold season. This latter period is in turn terminated by the beginning of the higher temperatures of spring and the second warm season, etc.

For convenience, the first warm season is subdivided into a first growth

period characterized by a rapid rate of growth of the young spiny lizard, and a second growth period, during which the rate of increase in length is appreciably lower. The decrease in growth rate that terminates the first growth period takes place roughly at the 45 mm snout-vent length stage. Since the second growth period is terminated by the first cold season, the maximum size of lizards included in this period would vary from one year to another. In this study, the greatest snout-vent length attained during this period was 51 mm. Coincidentally this is the maximum snout-vent length of the juvenile spiny lizard as defined above.

First warm season.—Increase in length of the young spiny lizard during the first growth period is believed to be more or less continual, the rate of this increase in head-body length ordinarily varying from .29 to .33 mm per day. Of 14 young lizards marked and recaptured one or more times over periods of from 25 to 46 days, six maintained relatively constant rates of increase in length, ranging between the above extremes (fig. 8). The growth of the remaining eight was retarded, perhaps as a result of the removal of toes for marking purposes. Five of these eventually showed signs of resuming a normal growth rate. Another, apparently suffering little ill effect from initial toe clipping, appeared to be adversely affected several weeks later by the inadvertent removal of a third toe (fig. 8, specimen U). Eighteen other juveniles captured two or more times during the summer but over periods of less than 25 days apparently increased in length at rates of between .13 and .40 mm per day. In view of the difficulties and possible inaccuracies involved in measuring a tiny kicking, squirming lizard with a millimeter rule, I have accorded but slight consideration to such increases in length recorded over short periods of time.

Since increase in length is retarded very much or stopped completely during the colder months of the year, the later the egg is hatched, the poorer will be the hatchling's chances of reaching the 45 mm head-body length stage and entering the second growth period within its first three months. The early advent of cold weather would, of course, further reduce its chances, but the late arrival of low temperatures would provide a longer growing season. Since the rate of increase in length of the juvenile varies but little during the first growth period, the length of the hatchling on leaving the egg is directly related to the length it may attain before the end of the growth season. Large individuals will have a considerable advantage over smaller ones. A large hatchling of 26.5 mm head-body length, for example, will normally reach the 45 mm stage in 8 or 9 weeks. A small specimen of 20.5 mm head-body length will require from slightly less than 11 to about 12 weeks to attain the same size.

The head-body length at which the first reduction in juvenile linear growth rate was observed differed from one individual to another but generally was between the 40 and the 50 mm stage. Arbitrarily, the 45 mm stage is used here to designate the beginning of the second growth period. Because only a small proportion of the juvenile lizards in a population enter the second growth period before they are overtaken by cold weather, data were obtained from a very few specimens over this period. Only one, or possibly two, juveniles in Study Area 1 were recaptured after this change (fig. 8, specimens AK and AS). More complete observations were made on four specimens

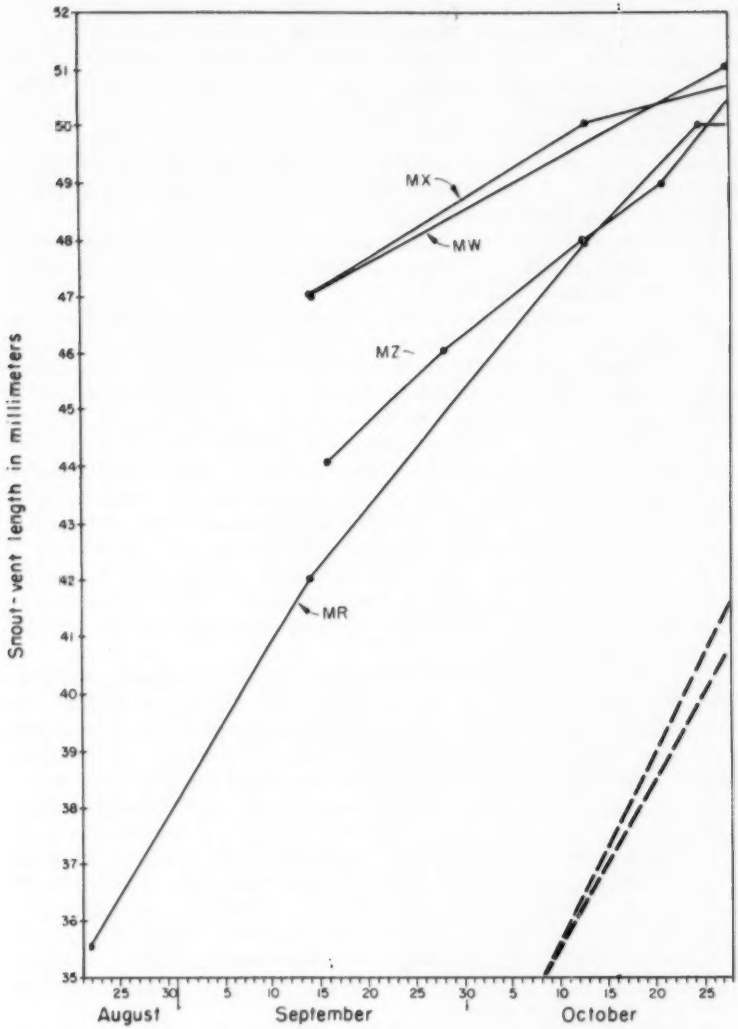

FIG. 9.—Increase in snout-vent length of the juvenile spiny lizard during the second growth period. Broken lines at lower right represent the normal rates of increase in snout-vent length of spiny lizards during the first growth period.

in Study Area 2 in the later summer and fall of 1949 (fig. 9). One of these, specimen MR, was captured at least once during the first period of rapid increase in length and, probably, three more times during the second period of slower linear development. The other three specimens were not taken until they had entered the second growth period. Growth rates of these

four juveniles ranged from .09 mm per day to .20 mm per day. Marking these individuals by the removal of toes may well have caused their rates of increase in length to be slightly lower than would otherwise have been the case. However, it is felt that the length of time over which these four specimens were observed (over one and one half months) was sufficient to permit essentially complete recovery. It is possible that factors other than age or size were responsible for the reduction in rate of linear growth observed in lizards during the second growth period. To assume that such was the case, however, would be to ignore the fact that in every juvenile over 45 mm in snout-vent length, the rate of increase in length was considerably lower than that observed in any juvenile under 40 mm in snout-vent length and captured on two or more occasions over a period of 25 or more days. It seems likely that the rate of increase in length is reduced gradually, producing a growth curve that tapers off slowly but steadily. Such a curve would be consistant with the upper portion of the logistic growth curve. Since the second growth period immediately precedes the young adult stage, a reduction in the rate of linear growth of the large juvenile might be expected as a result of the changes in physiology and body proportions involved in the transition from juvenile to adult.

First cold season.—During the winter of 1949, it was possible to follow rather closely the growth of several juvenile lizards in Study Area 2. Although the development of each of these was retarded or stopped by the first

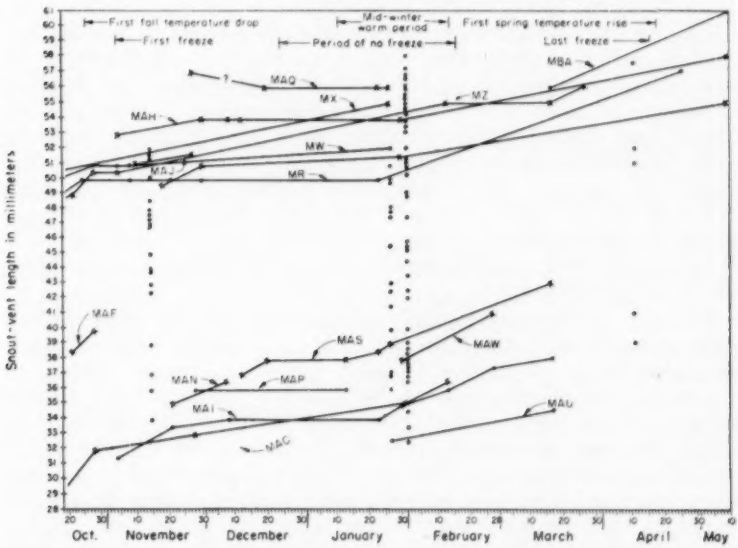

FIG. 10.—Increase in snout-vent length of the spiny lizard over its first cold season. Dots represent capture points for females, x's for males. Vertical rows of dots show size distribution of random samples of spiny lizards collected on the indicated dates. The apparent reduction in snout-vent length for specimen MAQ, indicated by a ? is probably due to error in measuring.

appreciable drop in maximum daily temperatures of the fall, there was considerable variation among them in the degree to which growth was affected later in their first cold season (fig. 10). In general, smaller juveniles tended to grow more during the cold months than did the larger ones. It is believed that the higher growth rate of smaller lizards was responsible in very small part for this. More important was the tendency on the part of smaller juveniles to enter hibernation later, emerge more frequently on warm winter days and become active earlier in the spring. Fitch (1940) observed that young Pacific fence lizards, *Sceloporus occidentalis*, remained active later in the season than did adults. Cowles (1941) found the same to be true of most species of desert reptiles and noted that one of the important reasons for this was "the effective heating of these small bodies in favorable periods which are apparently too brief for utilization by the adults. . . ." Although this principle certainly is operative to a greater or less extent and is apparently supported by observations of the southern spiny lizard in southwest Georgia, it is conceivable that the young are more eurythermal than the adults. In support of this, it was clearly indicated that juveniles continue normal activity at high summer temperatures during which adults took shelter and became quiescent. Whichever factor is the more influential, growth of the individual over the winter is closely related to the amount of heat available. Thus, lizards that were observed to have hibernating sites in the open scrub-oak forest, exposed almost constantly during the day to the sun's heat, increased in length more rapidly during the colder months than others overwintering in the heavily shaded hammock and at its edge.

The lack of variability in the linear growth rate patterns of juveniles over the warm months suggests that there is at this time a sufficient if not excessive supply of food for all. However, as food becomes more scarce in the winter, and as less time is spent in active foraging, it seems probable that the food supply becomes the basic limiting factor directly restricting growth. Conditions controlling activity periods, then, become of importance primarily in that they restrict the time during which growth may take place but not the rate of growth itself. It is felt that the variation in rate and amount of growth observed during the first cold season is in large part a response to the local variation in food supply and in those factors which influence activity periods.

Winter in south Georgia is quite mild as compared with more northern regions of the United States. However, reduced temperatures do extend over a considerable period of time. In 1949 temperatures began falling on October 26, and on the night of November 4, the first freeze was recorded. The last freeze of the season did not occur until April 16, 1950, and two days later temperatures were on the up-trend and were not to fall appreciably again that spring. Thus, the duration of the cold season was only slightly less than six months, and the period of time elapsing between the first and the last freeze was slightly less than five and one half months. During this lengthy cold period several short warm spells lasting but a few days, and one that persisted for more than a month, provided the spiny lizards some time for foraging and growth.

In the case of every juvenile followed closely over the cold season there were at least two and usually more periods of hibernation. The term hiber-

nation as it is here used simply refers to that habit possessed by many animals of becoming and remaining dormant (usually in a more or less sheltered situation) upon the arrival and continuance of cold weather. This dormancy is accompanied by reduced physiological activity. According to this definition, it would be possible for an animal to hibernate over a very short period of time, perhaps but a single night. Whether or not this actually occurred in Study Area 2 during the winter of 1949-1950 is not known, but climatic conditions were such that it might have. Maximum daily temperatures, excluding those of the mid-winter warm period, ranged between 41 and 84° F, usually from 55 to 75° F. Recorded daily minimum temperatures varied from 24 to 55° F. During this period, temperatures fluctuated commonly over a 30 to 40° span in a single day. It was not uncommon that temperatures of freezing and below at night would be followed the next day by readings of 70° F and above. Thus, for lizards having poorly insulated winter resting sites, there was opportunity for intermittent periods of hibernation. One juvenile lizard collected on November 18 while sunning was retaken three days later on November 21. For the three intervening nights minimum temperatures of 28, 25, and 35° F, were recorded. Since all nearby apparent hibernating sites offered but slight protection, it seems quite likely that the body of the small lizard was quite thoroughly chilled for at least part of the time between captures.

In general, juvenile lizards were observed to emerge from hibernation and become active at progressively lower temperatures as the cold season advanced. The moderate drop in temperatures at the beginning of winter brought growth to an immediate halt for most lizards. Subsequently, however, the same lizards were able to become active and grow at even lower readings. Probably the explanation for this lies in a seasonal variation of thermal requirements.

Very early in the cold season, young lizards utilized hibernation sites near which they remained for the duration of inclement weather. Although these sites were changed from time to time, those employed later were generally but a short distance from the original.

For the first three weeks of cold weather in 1949, temperatures remained fairly mild, and a few lizards could always be found on warm days basking in the sunlight about Study Area 2. The succeeding five and one half weeks' period, beginning about November 17, was much colder, with freezes occurring every third night on the average. As these conditions continued, lizards became more and more difficult to locate until on December 20, only two juveniles were collected. No lizards were observed during visits to the area on the 22nd and 28th of December when maximum temperatures were respectively 78 and 73° F. Presumably hibernation sites had been so chilled by repeated cold nights that these high mid-day temperatures could not warm them sufficiently to stimulate their dormant lizard inhabitants to activity.

Only one lizard was observed at a temperature of less than 60° F. This example was taken on November 18 at 2:50 p.m. basking in the sun. On this day the maximum temperature recorded in the shade was 59° F. Since this juvenile was exposed to the direct rays of the sun, its body temperature was very probably somewhat higher. Two other juveniles were observed at a temperature of 64° F, and ten were taken on days during

which the temperature did not rise above 65° F. All of these noted were basking in the sun in the early afternoon.

A period of unseasonably warm weather began abruptly on December 26 and continued through February 14. Maximum daily readings over this time varied from 59 to 83° F. with the temperature failing to reach 70° on but seven days. For the first part of this period, from December 26 to January 11, daily minimum temperatures were evenly distributed between 35 and 57° F, but, for the last month, low readings averaged considerably higher, ranging from 35 to 63° F, only six falling below 50° F. This last period is the one referred to as the mid-winter warm period in figure 10. A little over two weeks after the first high temperatures, lizard activity was again observed in the area. On this day, January 13, only two lizards could be found, and both of these, judging by a thin film of dirt over their bodies, had recently emerged from hibernation. Three juveniles taken on January 23 were similarly dirt-covered. The length of the time interval between the beginning of warm weather and subsequent emergence from hibernation is probably the length of time required for the hibernating site to become sufficiently warm to stimulate its occupant lizard to activity. This time would vary from one lizard to another depending on the total heating effect of increased temperatures, insulation of the hibernating site, and its location, that is, whether exposed to little or much direct sunlight. In addition, the sum total of heat required to stimulate emergence would be expected to vary from one to another individual.

Following the mid-winter warm period, cold weather began anew and continued until about April 18. This two months' cold spell differed from that preceding the mid-winter period of high temperatures in that it was not so severe. The first cold wave to move in was harsh enough to stimulate most lizards to retreat to hibernating quarters. Some of the larger juveniles did not emerge again for several weeks but a few smaller ones could always be found on warm days sprawled on logs and stumps in the sun. As spring approached, warm spells between freezes became progressively longer and milder. More and more lizards were observed basking and foraging, and measurable growth, though still intermittent, was observed in most juveniles.

Growth observed in juveniles over the winter of 1949-1950 was probably greater than would normally be the case. The mid-winter warm period was largely responsible for this, but even the colder periods were milder than in most years. For those lizards followed over the entire cold season, the head-body length was increased by between 3.5 and 6.5 mm. These were all large juveniles or young adults, and it is estimated that some of the smaller juveniles increased in snout-vent length to a considerably greater extent. One of these small examples (fig. 10, specimen MAS) increased in body length by 6 mm between December 12 and March 17, a period that included, in addition to the mid-winter warm period, the greater part of periods least conducive to rapid growth as indicated by the development of other lizards.

Juvenile and young adult lizards observed over the winter in Study Area 2 may usually be separated into two distinct size groups. Undoubtedly these size groups represent, in general, early and late broods of the previous summer, and probably first and second broods (fig. 10). The estimated time interval between hatching of the juveniles of these two groups is about right

for a second preoviposition developmental and incubation period following a normal early oviposition. Several series of spiny lizards were collected during the cold season at various localities in Baker County, Georgia. In order to present a more complete picture of size distribution over the winter, body measurements of the juveniles of these series have been plotted against their dates of capture in fig. 10. The series taken on November 15, 1949, January 25 and April 11, 1950, were not large enough to indicate more than that juveniles in Study Area 2 were roughly similar in size distribution. However, the series taken on February 1, 1950, was considerably larger. Two size groups, similar to those found in the Study Area, appear to be indicated.

Throughout their first summer, fall and winter, lizards hatched in 1949 could be easily distinguished from older examples by their smaller size. Although the largest first year adults (hatchlings in 1949) approached very closely in size the smallest second year adults (hatchlings of 1948) during the mid-winter warm period, no overlap of these size groups was found. At this time, the largest first year adult measured 56 mm in snout-vent length, the smallest second year adult 58.5 mm. Fortunately, this latter adult was a male and ventral color pattern could be used in estimating age. All other second year adults examined were 60 mm or more in head-body length. During warm spells at the latter part of the cold season, overlap of first and second year size groups was observed, but for several months thereafter a high proportion of the younger lizards could be readily distinguished from those of the preceding generation. The time of first overlap in size of first and second year size groups would vary from year to year depending on length of the first growth season and severity of the ensuing cold season, long growth seasons and mild winters tending to bring about early overlap, short growth seasons followed by rigorous winters, the reverse.

Second warm season.—The southern spiny lizard becomes fully mature shortly before or during its second warm season, that is, at less than one year of age. Most of these young adults mate for the first time during the late warm spells of their first cold season or early in the succeeding spring, as do the older adult lizards. Of seven females estimated to be less than a year old taken in May, 1950, five, each over 50 mm in snout-vent length, carried well developed eggs. The other two, one 44 mm, the other 46.5 mm in head-body length, contained only small ovarian follicles. Another first year female, originally captured and marked as a month old juvenile in August of 1949, was found to be gravid on April 26, 1950. At the latter date, she measured 57 mm in snout-vent length.

It was not possible to follow lizards completely through their second warm season, from the termination of one to the commencement of another hibernation period. However, since the cold season of 1948-49 was roughly similar to that of 1949-1950, a fair idea of development during the summer growth period can be obtained by treating together data obtained in the summer and fall of 1949 with that procured in the spring of 1950 (fig. 11).

Three young adults, known to be less than a year old and followed into the 1950 growth season, had attained body lengths of from 55 to 61 mm by May 10. These were all fairly large young representing early broods of the 1949 hatching season. The smallest second year adult followed into the 1950 growth season measured 60 mm in snout-vent length on May 3, thus indicating

slight overlap of age groups. Probably there was no extensive size overlap between first and second year adult groups before mid-June. The body length measurements of a series of young (first year) adults taken on May 23, 1950, are shown in figure 11. It will be noted that the first and second brood size groups were tending to merge at this time. This would be expected because of the more frequent emergence from hibernation and higher growth rate of smaller lizards during the winter. In the late warm spells of the cold season, all young adult lizards increased in length to some extent, and such growth continued for a time into the ensuing warm season.

If the rate of increase in length of first year adults during the early part of their second growth season were to continue throughout the summer, it is evident that virtually all would exceed the known maximum length by the end of the warm season. Since such is not the case, it seems likely that the intermittent pattern of growth observed for first year adults during July, August and September of 1949 (fig. 11) may be similar to the growth pattern earlier in the warm season. Three of six lizards which were followed over the last half of June, 1948, in Study Area 1 showed no increase in length during June followed by moderate to rapid growth in July. A series of lizards taken on May 23, 1950 (fig. 11), when compared with marked lizards followed into early May, 1950, suggests that the intermittent pattern of growth had already begun at that time.

Observations made during the middle and latter part of the warm season suggest some of the factors that contribute to the growth lapses observed. Probably, courtship was not an important cause since the major part of this activity had taken place somewhat earlier, in March and April. It was observed that both ecdysis and oviposition were generally preceded by periods

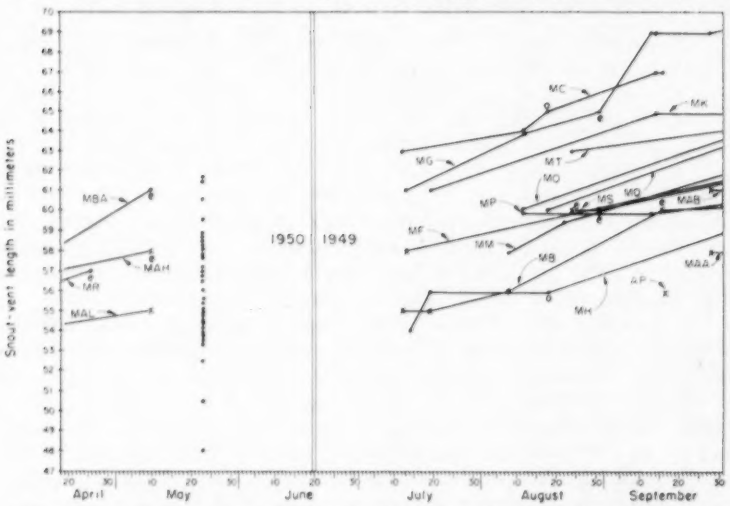

FIG. 11.—Increase in snout-vent length of the spiny lizard during its second warm season. Dots indicate females, x's males; vertical rows of dots represent series of spiny lizards collected in the general area. Captures following oviposition are indicated by o's, those following ecdysis by e's.

of little or no increase in length. The rate of increase in length of first year adults was usually lower than that of juveniles. With a few exceptions, this rate varied from about .06 mm per day to .13 mm per day for periods of growth not affected by molting, oviposition or injury. One large female increased in snout-vent length at the surprising rate of .30 mm per day (approximately) for almost two weeks (fig. 11, specimen MG).

The retardation of growth preceding oviposition was considerably more pronounced than that occurring prior to ecdysis. Previous to molting, growth was rarely affected for more than a week, whereas little measurable increase in length could be found for the last two to four weeks of the preoviposition developmental period (fig. 11).

Thus, for females at least, growth would be retarded or stopped for several weeks in late spring or early summer prior to oviposition and again in late summer for those depositing second clutches. An estimated two or three molts in the course of the growth season would involve another week or more of negligible development. These factors, combined with the general reduction in rate of increase in length, probably limit growth of most first year adult females to between 10 and 12 mm during their entire second warm season. Very small lizards would not breed before mid-summer and, with their more rapid growth rate, might increase in body length by as much as 15 or 20 mm.

Apparently, the first year adult male increases in length even less during the warm season than does the female. This is indicated by the greater discrepancy in size of males and females at the end of the growth season as compared with the differences at the beginning. Ordinarily, it is expected that males increase in snout-vent length over this period by between 7 and 9 mm, the smallest ones by as much as 18 mm. The reasons for the disparity in size increase between males and females are not clear. During the summer of 1948 in Study Area 1 it was found that first year adult males, even relatively small ones, failed to grow appreciably over periods of time up to two and three weeks duration. It is quite possible that these periods of inappreciable growth in the summer are related to the habitual wandering of the male. This constant movement of male lizards made it very difficult to observe an individual with any frequency and, thus, is largely responsible for the inadequacy of data on the growth of this sex.

There is some question as to whether the individuals shown in figure 11, under observation during July, August, and September, are all first year adults as is indicated. Certainly there can be little doubt regarding the smaller individuals since there was no size overlap between this and the contemporary juvenile age group. By projecting backward known growth rates, it becomes apparent that even the largest lizards estimated to be first year adults, observed in mid-summer, fall well within the size group of first year adults of known age observed in the spring. A single marked individual of known age was equivalent in size to some of the largest representatives of this age group. This specimen will be mentioned in more detail subsequently. Another specimen, a male, was originally marked as a hatchling of 24 mm snout-vent length on July 26, 1948 in Study Area 1 (fig. 8, example AP). This specimen was retaken on August 29, 1948 and found to have had a normal juvenile rate of growth. Specimen AP was retaken

at the termination of its second warm season on September 17, 1949 and found to measure 56 mm in snout-vent length (fig. 11). At this time, it was slightly smaller than the smallest specimen of equivalent age in Study Area 2.

Second cold season.—The growth of year old young adult lizards was affected somewhat earlier than that of juvenile lizards in the fall of 1949. Juvenile development was retarded in late October at the same time that daily maximum temperatures began a steady downward trend from the average summer 85 to 90° F. highs. Adult growth, however, was interrupted about the middle of September, perhaps by temporary drops in minimum daily temperatures to below 60° F. At this time, daily maxima continued relatively high. For a few adults which were under observation over the cold season in Study Area 2, it seems probable that there was no increase in length for the seven months following the September cessation of growth (fig. 12). One lizard did not increase in length measurably from mid-October to mid-April, and, quite probably, others followed the same pattern. However, most second year adults were able to resume growth for short periods of warm weather during the winter. The greatest total increase in head-body length recorded for specimens over the second cold season was 2 mm; the average was about 1 mm.

Growth in length of overwintering adults appeared to be influenced by the same factors that affected juvenile development over the cold season. For several reasons the increase in length of these older adults was neither as

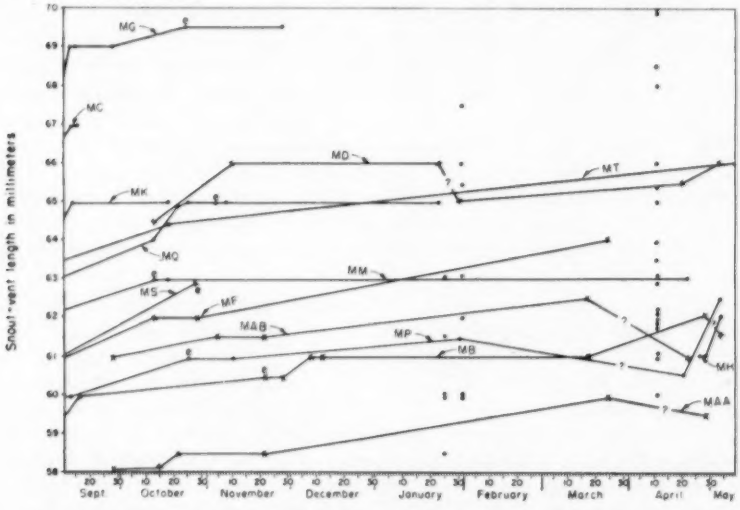

FIG. 12.—Increase in snout-vent length of adult spiny lizards during their second cold season. Dots indicate females, x's males; vertical rows of dots represent series of spiny lizards collected in the general area. The several instances of apparent reduction in snout-vent length, indicated by ?'s, may be due either to error in measuring or, if real, to sudden increase in body volume which would cause greater curvature of the vertebral column thus shortening the snout-vent length.

great nor as variable as that of younger lizards. As pointed out above adults enter hibernation earlier, emerge less frequently and for shorter periods than juveniles. Hibernation sites of adults are frequently in more heavily shaded areas than those of young lizards. Adults overwintering in the more open scrub-oak area were able to emerge from hibernation, become active and resume growth more frequently than those in the more densely shaded hammock. As with the younger lizards, adults were observed to wander but little during the winter and were able to tolerate progressively lower temperatures as the cold season progressed.

Third warm season.—A series of adult lizards taken on April 11, 1950, a short time before the beginning of the third warm season, provides some idea as to general size distribution of the group approaching two years of age (figs. 12, 13). Probably one or two of the largest specimens of this series are nearing their third birthday, but this could not be determined without a greater knowledge of the growth of each individual. Actually, this is of little importance since the maximum body size indicated, 70 mm, can be attained by lizards before the beginning of their third warm season.

On April 17, 1950, a marked adult female of the size group beginning the third warm season was collected in Study Area 1, (fig. 13, example AH). She had been first captured as a recently hatched juvenile of 27 mm snout-vent length on July 20, 1948. Subsequently, the same lizard was taken on August 16, 1948, and was found to have had a relatively normal juvenile growth rate. This specimen was not observed again before the April, 1950, collection, one year and eight months after the original capture. At this time, she measured 65.5 mm in snout-vent length and was, thus, equal in length to some of the largest lizards, of those believed to be completing their

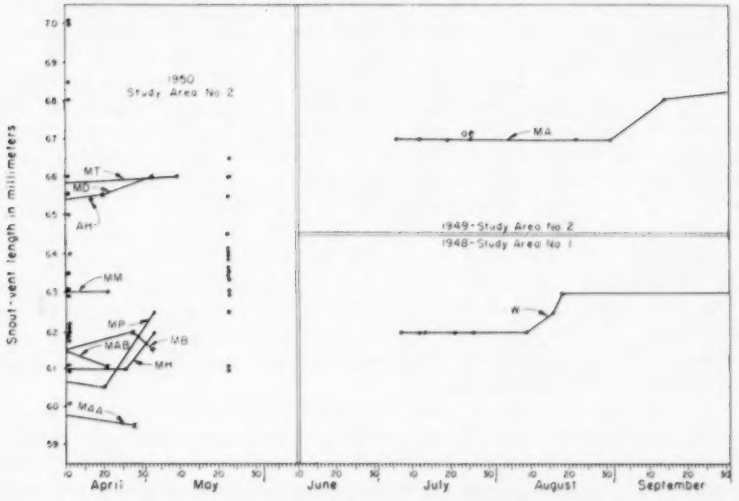

FIG. 13.—Increase in snout-vent length of spiny lizards during their third warm season. Dots represent females, x's males. The vertical rows of dots represent series of spiny lizards collected in southwest Georgia.

second year, which had been followed over the winter in Study Area 2. Two lizards, believed to be of the same age group, had attained even greater head-body lengths seven months earlier at the beginning of the cold season (fig. 12, examples MG and MC). On the basis of the above observations it can be assumed that most southern spiny lizards will attain, before completing their second year, body lengths in excess of 60 mm and up to 65.5 mm—assuming, of course, normal climatic conditions over the period. It is also strongly indicated that body lengths of 70 mm would be reached by some specimens in this same period (figs. 11, 12, examples MG and MC).

Since the maximum snout-vent length recorded for the spiny lizard in southwest Georgia is 70 mm (65.5 mm for the male), it follows that the third warm season for most individuals must involve very little increase in length.

On emerging from hibernation in the late warm spells of the cold season, lizards began pairing off almost immediately, and before mid-April, 1950, many paired lizards had been observed. Toward the last of April, growth was resumed by adult lizards, beginning their third warm season under observation in Study Area 2. Two of three males followed into May, 1950, showed no measurable growth although all three females under observation increased in length during this same period (fig. 16, males MB, MD, MAA; females MH, MP, and MT). Size distribution of a series of lizards believed to be of the same age group collected on May 23, 1950, suggests that the early resumption of growth may have been short lived. This is further supported by the fact that six of the eight females taken on May 23, 1950, were heavy with eggs, and, as pointed out earlier, appreciable growth usually ceases sometime prior to oviposition.

In Study Area 2, only one of the twelve adult lizards taken during July, 1949, had a body length in excess of 64 mm. This individual, a female, measured 67 mm. from snout to vent on July 6 at first capture (fig. 13, example MA). On August 31, she had not gained perceptibly in length. During this same time, from the first of July to the last of August, all but one of the other adults in the area had increased in length by between 2 and 4 mm. Two weeks after the August 31 capture of specimen MA, it was found that she had added a single millimeter to her head-body length, and a fraction more was added before she entered hibernation. The limited growth during the warm season and the unusually large snout to vent measurement of this example so early in the summer leave little doubt that she was a second year adult. There were further characteristics that set her apart from other adults in the population. First, she was far less agile and more easily captured than most, and second, though collected eight times over a period of nine months, she was never observed more than ten feet from the location of her first capture.

During the summer of 1948 in Study Area 1, a strikingly similar female was observed (fig. 13, example W). Although considerably smaller, 62 mm in head-body length, her growth characteristics and habits were very similar. This example was collected nine times over a period of eight months, always on or adjacent to the same tree and usually on a particular limb. From initial capture, on July 7, until August 9 she did not grow appreciably but by August 18, a single millimeter had been added to her

head-body length. No further growth occurred during the remainder of the warm season. It is believed that this female, in spite of her small size, was in her third warm season, about two years of age, at first capture.

As mentioned above, one other lizard beside specimen MA in Study Area 2 failed to grow in snout-vent length during the month of August, 1949. The late summer growth pattern was, in fact, quite similar to the two specimens thought to be two years of age (fig. 11, example MP). During the cold season of 1949-1950, however, her growth pattern was that of a year old adult (fig. 12, example MP) and quite unlike those of the two specimens believed to be two years of age, as will be indicated below. In addition, she was always quite alert and difficult to capture and, thus, in this respect also, unlike the old adults. Explanation for her lack of growth in body length during late summer may lie in the loss of a considerable portion of her tail at initial capture. Very likely, the rate of regeneration of this appendage, about .37 mm per day, consumed the greater part of available growth energy.

The relative abundance of adult spiny lizards in the early part of their third warm season is of some interest in view of their scarcity in late summer populations. It is suspected that predator action is responsible for the elimination of the greater part of this age group. The tendency of larger lizards to become less alert and more sluggish would make them increasingly vulnerable to attack by the predators, which are all too abundant in the habitat of the spiny lizard.

Although little can be said with certainty regarding total increase during the third growth season, it seems likely that 3 or 4 mm is about the average.

Third cold season.—Both of the above two year old adults that were followed over the latter part of the third warm season, were recaptured the following spring after emergence from hibernation. Probably hibernation sites were entered early and not quitted before the succeeding warm season. Neither lizard had increased perceptibly in length over the cold season, and both were found, on emergence from winter quarters, in the same specific locality they had frequented the previous summer.

Frequent examinations on warm winter days of the area usually inhabited by the larger of these two lizards, example MA, in Study Area 2, were never rewarded by a view of this specimen. That she was hibernating nearby is indicated by a recapture on April 26, 1950, at which time she was found on the tree of her first capture. Only one winter trip was made to the locality inhabited by the smaller female, example W in Study Area 1. At this time, however, weather conditions were unfavorable for any lizard activity, and none was observed. The following spring on March 20, 1949, she was found on the limb upon which she had been previously observed so often. She was not observed subsequently.

TAIL GROWTH

In the hatchling spiny lizard the tail occupies from about 46 to 58 per cent of the total length. In general, the longer the hatchling, the greater is the proportionate tail length (fig. 14). Presumably the tail of the very small hatchling grows in length at a much faster rate than the body for the

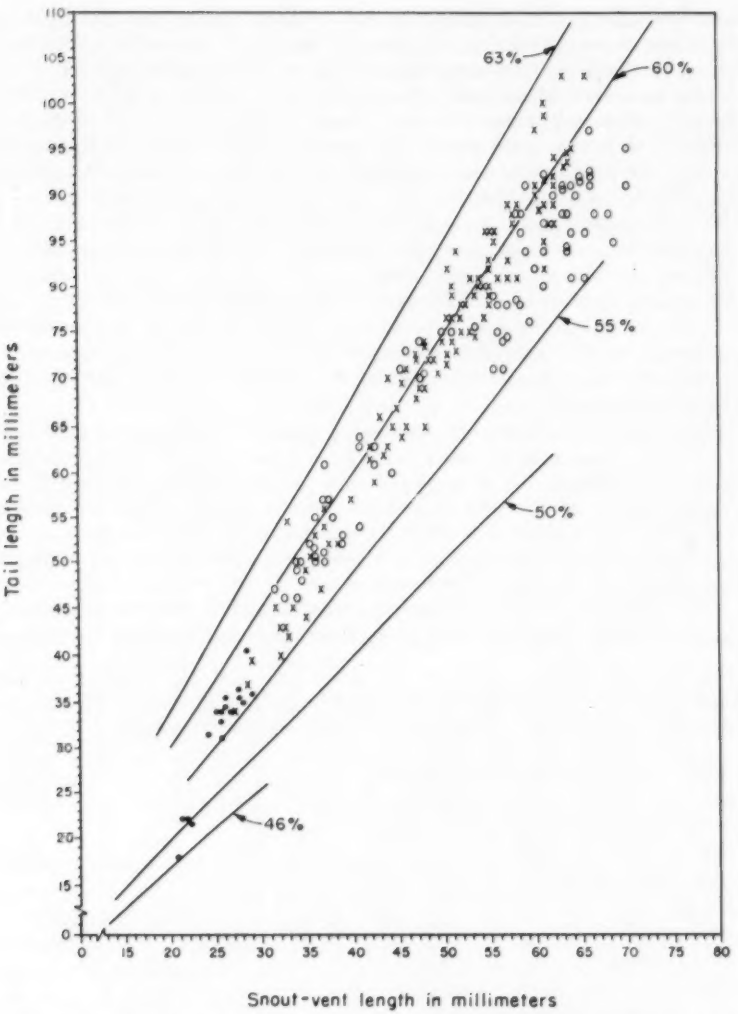

FIG. 14.—Ratio of tail length to snout-vent length in the southern spiny lizard. Dots represent unsexed juveniles, o's females and x's males. Percentages shown indicate the proportion of total length comprised by the tail.

first few weeks, since in all lizards examined except newly hatched examples, the unmutilated caudal appendage occupies more than 55 per cent of the total length. Throughout the juvenile growth period, the tail was found to grow only when the body was increasing in length but always at a slightly greater rate. The ratio of head-body growth to tail growth found for individual juveniles varied between .65:1 and .81:1, the former being closer to

the average for the entire juvenile growth period. In the late juvenile (head-body length of 40 mm or better), the tail was found to comprise between 57 and 63 per cent of the total length. Up to this late juvenile stage, there was complete overlap in relative tail length of males and females.

In the course of adult growth, the tail of the male continues its rather high rate of growth in length, relative to that of the body. The tail of the female, however, occupies a progressively lesser proportion of the total length. Probably the ratio of tail growth to body growth does not drop below 1:1. Until maximum length is attained, there is some overlap in the percentage of overall length occupied by the tail of males and females. At the 60 mm body length stage, the tail of the male was observed to comprise between 57 and 62 per cent of the overall length, that of the female between 55 and 61 per cent. There were not enough examples of very large males taken to determine accurately if there continues to be overlap in proportionate length of tail of males and females of maximum size. It is expected that there is very slight overlap in lizards over 158 mm in total length. Tails of females of this size constituted from 56 to 60 per cent of total length, those of males from about 60 to a little over 62 per cent.

As was the case with increase in length of the head and body and undamaged tail, regenerative growth was found only during the warm season and warm spells of the cold season. The maximum rate of regenerative growth observed, .71 mm per day for twenty-one days, was much more rapid than the rate of increase in length of either the head and body or the tail. It has been pointed out (Thompson, 1945) that regenerative growth accords with the typical logistic growth curve. Only three of the spiny lizards for which regenerative growth data are available were captured frequently enough to show a definite growth pattern (fig. 15, examples M, N and MM). The growth pattern of these three is clearly consistent with the S-shaped growth curve.

The rate of regeneration appeared to be determined primarily by the relative length of the lost portion of the caudal appendage. Generally, the greater the proportion of tail missing, the more rapid was the rate of replacement (fig. 15). Data presented by Thompson (1945) on tail regeneration in tadpoles shows that the rate of regeneration in these animals also is dependent upon the proportion of tail lost. The age of spiny lizards suffering tail losses appeared to have surprisingly little effect on the rate of regeneration, adults being capable of almost if not quite as rapid regeneration as juveniles. In lizards losing less than 10 per cent of the tail, no perceptible regeneration was observed though there were indications that, in such cases, the portion remaining attached was stimulated to unusually rapid increase in length.

LONGEVITY

The ecological life expectation of the spiny lizard in southwest Georgia seems to be considerably shorter than that of the other spiny lizards. Fitch (1940), in his study of *S. occidentalis*, estimated that one example which was collected in five successive years must have been nearly six years old at its last capture. A life span of over eight years is recorded for *S. graciosus gracilis* (Stebbins, 1948), and Kauffeld (1948) reported that one of a series

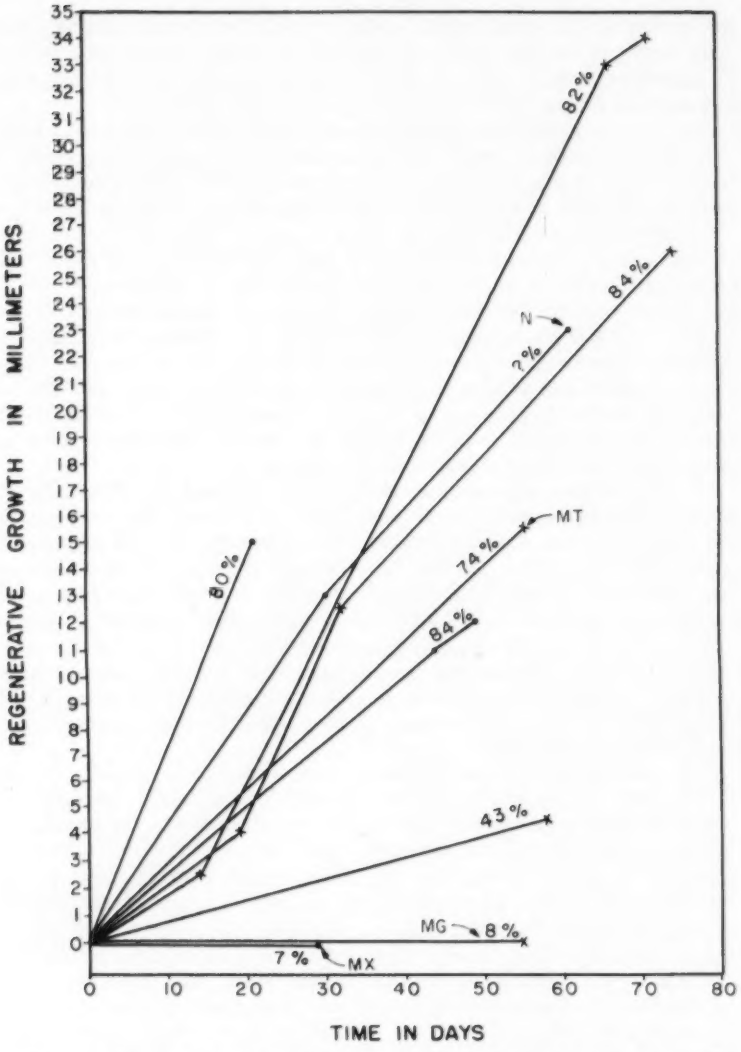

FIG. 15.—Regenerative tail growth of the spiny lizard during the warm season. Dots represent capture points of juveniles, x's of adults. Percentages indicate the proportion of caudal appendage lost.

of marked *Sceloporus undulatus hyacinthinus*, was recaptured almost five years after its release.

It was shown above that the southern spiny lizard may attain maximum size before two years of age. In considering total populations for the last half of a warm season, it was found that spiny lizards two years of age

and older made up between 1 and 2 per cent of the total number of individuals. For example, in and adjacent to Study Area 1 from June 15 to September 15, 1948, the ratio: juveniles—adults in their 2nd warm season —older adults was 48:13:1. Since visits to the area were discontinued before all eggs had hatched, the number of juveniles indicated is low. In Study Area 2 over the same period in 1949, the ratio of juveniles to year old adults and to older adults was 5:14:1. The number of juveniles found over this period is obviously very low and could not reasonably represent more than a fraction of the young produced by the adults in the area. Marking studies over this period showed that very few juveniles had begun to move into the hammock of Study Area 2 (or out of the scrub-oak forest of Study Area 1). The ratio of year old adults to older spiny lizards was about the same in both areas.

Both of the marked spiny lizards, thought to be about two years of age and in their third warm season at first capture, survived the following winter and were probably about two and one half years of age at last capture. Since their disappearance in spring coincided with a general reduction in numbers of the population, it seems likely that they were eliminated, along with many younger adults, perhaps by predator action. There was observed during this period a marked increase in the activity of two reptiles well adapted to prey on the spiny lizard, the black racer, *Coluber constrictor priapus,* and the coachwhip, *C. f. flagelleum.*

From the above evidence, it is apparent that a very small proportion of the spiny lizards in the area studied completed their second year. In view of the sluggish nature of two year old adults, it is improbable that more than a very occasional individual survives its fourth warm season. Although half a dozen trips were made to Study Area 1 during the latter half of 1949 and early 1950, the only lizards recaptured were those originally marked as juveniles during the summer of 1948. The indicated relatively short maximum life expectation of the southern spiny lizard as compared with the northern sub-species, may be largely a result of the longer growth and activity period of the southern race. Such an explanation would be consistent with the principle pointing out the inverse proportion between length of annual activity season and longevity and known as Rubner's hypothesis (Allee *et al.* 1949).

The ecological longevity of the newly hatched spiny lizard is undoubtedly very short, probably less than six months. Naturally this will vary from one area to another, even locally, and from year to year. Data obtained in Study Area 1 during the summer of 1948, provide a general idea as to the rate of elimination of juvenile spiny lizards. Since the young move about to some extent, it was necessary to assume that for every lizard moving out of the area, one had entered it. Then by comparing the number of examples taken in the area in each weekly age-size group of lizards hatched during a particular period, the rate of elimination of juveniles in their first few weeks of life was approximated. Juveniles moving into the area were assigned an age based on average juvenile growth rate and hatchling size. Sixteen lizards, one week old or less, were taken in the area between June 21 and July 31, 1948 (fig. 16). The decline in numbers of this age group during subsequent weekly periods was slight though fairly steady for the first month, at which time losses per week increased. Of the six to seven weeks old group, be-

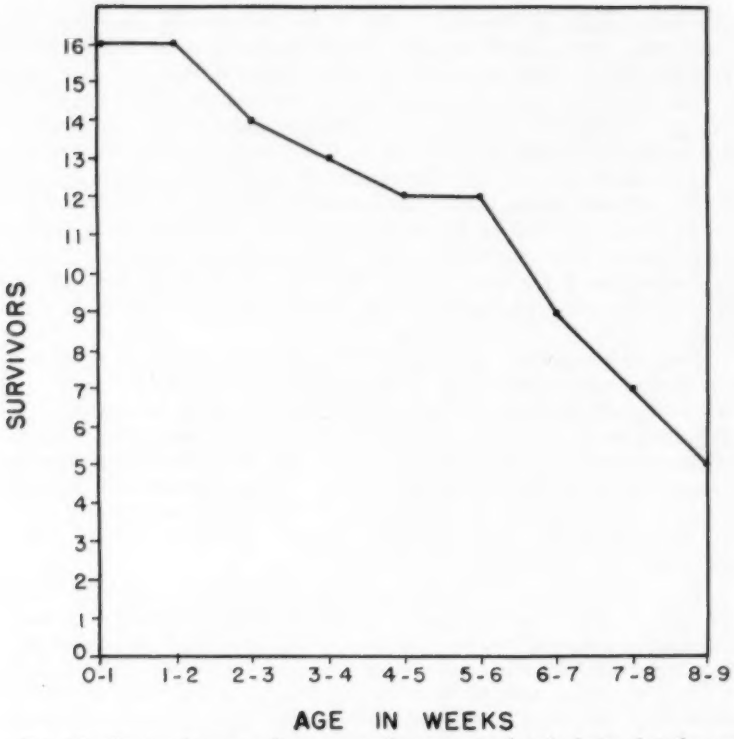

FIG. 16.—Survivorship curve for a group of young spiny lizards during their first two months of life. At least four of these juveniles survived their first cold season and were over seven months of age at last capture.

lieved to have hatched in the June 21 and July 31 period, only nine were collected in the area. Thus slightly less than 50 per cent of these young were eliminated in one and one half months. Only five examples of the eight to nine weeks old group were taken, indicating a loss of about 68 per cent of the juveniles in their first two months. There was no evidence suggesting unusually high mortality of juveniles immediately after hatching. Rather, an increased rate of loss was found after lizards had developed somewhat but were still fairly abundant. During the cold season the mortality rate was very low. At least four of the juveniles marked over the June 21 to July 31 period survived hibernation and were taken in the area after March, 1949. Mortality data for older lizards are not so complete as for the very young; however, it was indicated that the greatest adult losses occur during the early part (May and June) of the warm season.

SUMMARY

A field investigation of the life history of *Sceloporus u. undulatus* was carried out in southwestern Georgia during two periods, April to September, 1948 and July, 1949, to May, 1950.

The longest male spiny lizard measured was 168.5 mm in length, 65.5 mm in head-body length. The longest female was 165 mm overall with a snout-vent length of 70 mm. Maximum head-body lengths found for spiny lizards in the area studied were not as great as those reported for examples of *S. u. undulatus* from other areas and for specimens of the northeastern *S. u. fasciatus*.

Three different types of melanism were observed in spiny lizards. One of these appeared to be a temporary condition correlated with low temperatures and moist conditions; another was developed with increasing age. A third and more extreme type was characteristic of certain individuals and may have a heritable basis.

Examination of 191 specimens from three spiny lizard populations strongly suggests a clinal reduction in dorsal scale count from populations northwest of the Flint River to populations southeast thereof, and a higher mean dorsal scale count for females than for males in each population.

The preovipositional developmental period is about 40 days in duration.

Eleven clutches of eggs contained from 6 to 10 eggs each, averaging 7.6 eggs. The earliest oviposition date recorded was May 2; the latest occurred sometime after July 25. Various evidences suggest that two egg clutches may be deposited in a single season.

Laboratory incubation periods of 49 and 58 days were found for eggs.

The first hatchling of the season was taken on June 21, the last on September 5. It is very probable that some eggs hatched after the middle of September.

The hatchling ranges from 38.5 to 61.5 mm in overall length, from 20.5 to 26.0 mm. in snout-vent length.

During the first warm season, juveniles may increase in head-body length by more than 25 mm at rates of up to .33 mm per day. During subsequent warm seasons total increase in snout-vent length is much less and may amount to less than 3 mm in the third warm season.

The southern spiny lizard becomes sexually mature before or during its second warm season and, thus, before the completion of its first year.

Growth in head-body length was found to be retarded prior to oviposition and ecdysis. Periods of growth of the adult male appeared to be less frequent than those of the adult female.

The effective cold season was found to extend from about five and a half months for juveniles to as much as seven months for some adults. An observed greater total increase in head-body length of small lizards, as compared with large lizards, during the cold season is believed to be a result of more frequent periods of foraging during the winter. More frequent emergence from hibernation on the part of juveniles may result from a lower activity threshold temperature and the rapidity with which their small bodies may be heated to this threshold temperature.

The rate of increase in tail length was found to exceed slightly the rate of increase in body length. The ratio of tail growth to head-body length increase ranged from 1:.65 in some juveniles, to almost 1:1 in the old adult female lizards.

The rate of regenerative tail growth is apparently determined by the proportionate length of the lost section of tail. This rate of increase in

length was found to vary from inappreciable, in lizards losing less than 10 per cent of the tail, to .71 mm per day in one lizard which had lost 80 per cent of its caudal appendage.

The maximum ecological life expectancy of this form appears to be about three years, the average, something less than six months.

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Yearly Food Habits of the River Otter in the Thompson Lakes Region, Northwestern Montana, as Indicated by Scat Analyses[1]

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Otters (*Lutra canadensis*) have been protected in Montana since the 1949-50 trapping season but there is evidence that a few are unintentionally taken in traps and some may be eliminated by acts of vandalism. Unfounded reports from Lincoln County indicated these animals are undesirable. Some fishermen claim they reduce the number of trout and bass and thus contribute to poor fishing. Some trappers declare otters destroy muskrats, beavers and minks. A survey of the literature did not reveal information to substantiate or refute these claims so it seemed desirable to make further studies on the otter.

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The Study Area

The investigation was centered around Thompson Lakes, a group of 31 lakes and streams, situated approximately 40 miles southeast of Libby, Montana (fig. 1). These lakes are easily accessible and many can be seen from U. S. Highway No. 2.

Table 1.—Relative abundance of fish in study area as indicated by limited sampling.

Area and Date	Sampling Method	Catch
Thompson (9 sampling areas, see fig. 1) June-Aug.	7 hr. fishing (4 areas)	50 YP in 2 hrs., 100 SF in 3 hrs., 10 SU in 1 hr., 12 CRC, 8 SF in 1 hr.
Sept. 3	electric shocking (2-100 ft. stream sections)	76 SC, 21 SU, 16 T, 10 S, 7 WF, 3 SH
June-Sept.	70-24 hr. gill net sets (1 area)[2]	(av. catch per 24 hr. set) 63 YP, 35 WF, 17 S, 7 SF, 1 SU
May, Aug.	13-24 hr. sets (3 areas)	28 SF, 22 S, 14 CRC, 6 B, 3 T, 2 WF, 1 SU
Gary's (1 area)	2 hrs. fishing	4 SH, 2 T

B—bass, CRC—Columbia River chub, S—sucker, SC—sculpin, SF—squawfish, SH—shiner, SU—sunfish, T—trout, WF—whitefish, YP—yellow perch.

[1] A joint contribution from Montana State College, Agricultural Experiment Station, Project No. MS844, Paper No. 313 Journal Series and the Wildlife Restoration Division, Project W-49-R, Montana Fish and Game Department.

[2] The data of 70 gill net sets were supplied by John Echo while working on a fish study in the lower Thompson Lake.

Fishes native to the area include: Dolly varden trout (*Salvelinus malma*), cutthroat trout (*Salmo clarkii*), rocky mountain whitefish (*Prosopium williamsoni*), Columbia coarse scaled sucker (*Catostomus macrocheilus*), Columbia long-nosed sucker (*C. catostomus*), red-sided shiner (*Richardsonius balteatus*), sculpin (*Cottus punctulatus*), squawfish (*Ptychocheilus oregonensis*) and Columbia river chub (*Mylocheilus caurinus*). Hybrids between the latter two were common. Exotics include: Kokanee salmon (*Oncorhynchus nerka*), eastern brook trout (*Salvelinus fontinalis*), rainbow trout (*Salmo gairdnerii*), largemouth bass (*Micropterus salmoides*), yellow perch (*Perca flavescens*), and pumpkinseed (*Lepomis gibbosus*). According to Echo (personal communication) there exists an overpopulation of perch and sunfish.

Gill nets, electric shocking equipment and fishing were employed to obtain information on fish abundance in the various waters (table 1). An indication of muskrat (*Ondatra*), mink (*Mustela*), and beaver (*Castor*) numbers was afforded by "sign" (table 2).

Gary's Lake, about 20 miles due north of the Thompson Lakes area was included for comparison because it is somewhat isolated and supports a greater concentration of fur bearers.

On three occasions only were pairs of otter observed within the study areas.

TABLE 2.—Relative abundance of fur bearers in study area as indicated by "sign."

Area	Av. no. beaver houses	"sign" Beaver	Muskrat	Mink
Thompson (9 sampling areas)	1.3	X	XX	X
Gary's (1 area)	3.0	XXX	XXX	X

X—Light, XX—Moderate, XXX—Heavy.

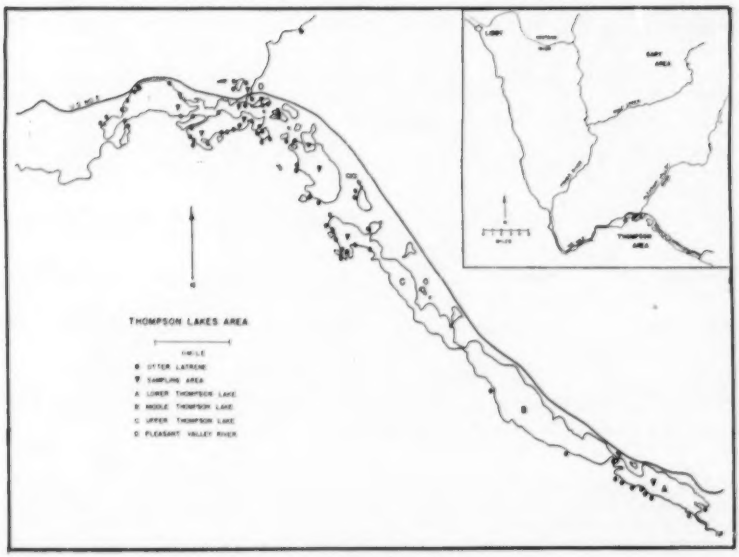

Fig. 1.—Map of study area.

Few sight records were reported. Liers (1951), observed dens of three litters along a 20 mile stretch of stream in Minnesota. No dens were seen in this study. Two otter were observed on a small lake (8 acres) for 2 hours. They were not observed to eat anything. During the 5-10 minutes they were on the shore they deposited 3 droppings. This one direct observation was not sufficient to determine the number of scats deposited by an otter in a given length of time. The number of scats collected at latrines between known dates, and known or estimated dates of scat deposition, revealed few otter in the area. Those present usually remained only a day or two in any one locality. According to Liers (1951), "Individuals may cover 50 to 60 miles of stream course in a year. Families range about 3 to 10 miles in a current season." The extensive home range of the otter in the study area is indicated by the dates scats were deposited at known latrines. During spring, the deposits seemed to show a visit to an area for a day or two, absent 2 or 3 days, return for a day and absent 2 or 3 days. This pattern was repeated 3 or 4 times then an absence between visits of 7 to 15 days occurred. The frequency of visits decreased as summer progressed. Scat evidence indicated that otters deserted the lakes when they became frozen over. The fact that droppings were deposited on the same day at Gary and Thompson areas, separated by 28 water miles, indicated each of these areas served as separate home ranges for the otter inhabitants. The number of otters estimated to use the study area was 6-8.

METHODS

"Pulling out" places and latrines (Liers, 1951) were located by walking the shores. Most latrines were on the shores, several were on or near beaver houses. Fallen trees, larger than 18 inches in diameter, extending from the shore into the water were often used. Latrines appeared to be of long establishment.

Otter scats are readily recognized with experience. The average is approximately ¾ inch in diameter and characteristically in 2, 3, or 4 curved segments each about 1½-3 inches long making a total length of 4-7 inches. It is not unusual for droppings to vary in size from above average to a remnant. Fresh droppings were usually black with a strong characteristic odor. They usually consisted of fish scales and bones although other materials such as hair, feathers etc. were frequently present. Heavy mucus was mixed throughout a fresh scat. Drying, crusting and decrease in mucus content progressed with age. To determine the rate of change, fresh scats were tagged, left unmolested and revisited daily. Droppings from immature otter could be mistaken for those from a large mink if it were not for the smaller diameter of the latter and the characteristic one segment (fig. 2).

An occasional "sign" noticed at a latrine site was a white discharged substance. Some trappers reported this to be "phlegm" from an oral discharge. It was usually found separate from the scats but in their vicinity. It had an irregular form (⅛ to ¼ inch thick and 1 to 2 inches long), white opaque color, elastic quality and apparently was lacking in odor. A yellow tinge accompanied aging. One trapper was reported to have used this material to make scent for trapping otter.

When a latrine was discovered all scats were aged and placed in separate envelopes on which essential data were recorded. Once the location of a latrine was established it was visited regularly for scat collections. Eight were located

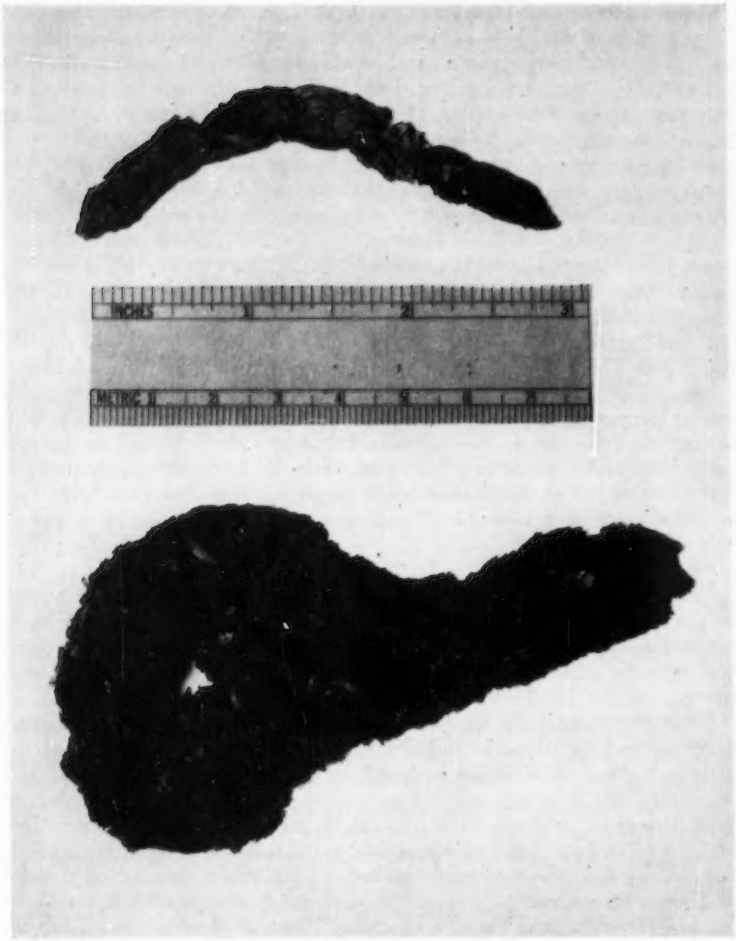

Fig. 2.—Otter scat above, mink below.

at Gary's Lake and 88 on the Thompson study area. Snow made accessibility to the areas difficult throughout the winter and fall but 6 collections were made. Final collections were made after all snow disappeared and "lost" droppings were recovered. A total of 2209 scats was collected from April, 1952, through May, 1953. The approximate date of deposition was determined for 1374 which constitute the basis of this study.

Analysis of droppings was accomplished in the dry state. Scats were broken apart in a culture dish with dissecting needle and tweezer and examined under a binocular microscope. Smaller items, such as hairs and parts of feathers, were reexamined under the compound microscope. The complete scat was searched

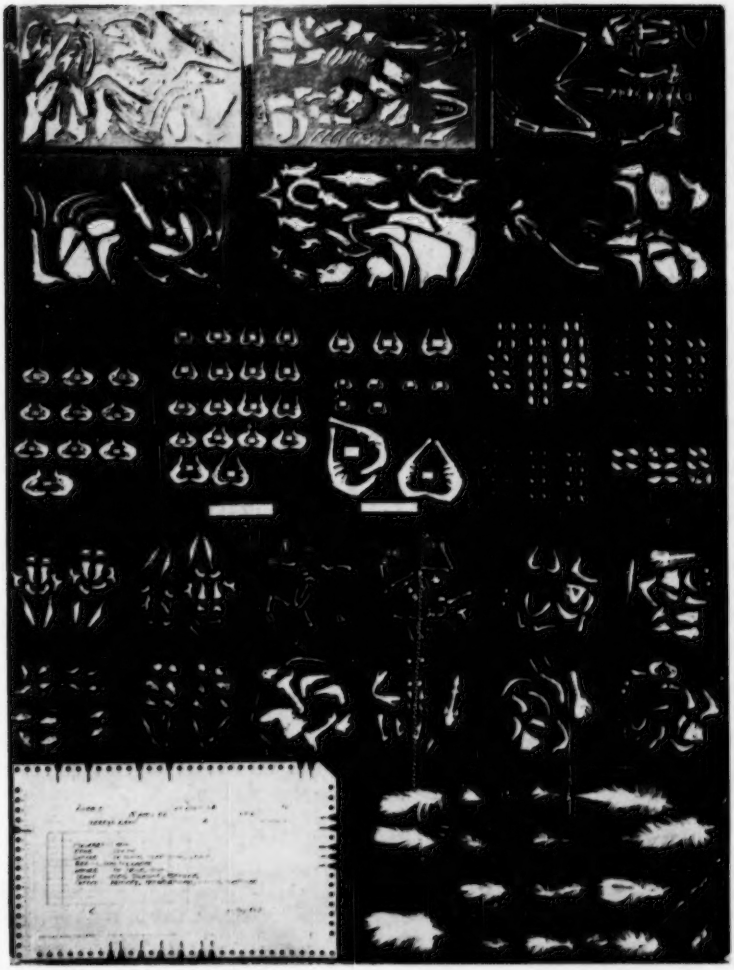

Fig. 3.—Representation of reference collections used to identify diagnostic items found in scats.

for recognizable remains of items in the diet. These were identified by comparison with reference collections of bones, hair, feathers, and other undigestible materials of vertebrates and invertebrates. Identified items were recorded on the collecting envelope, placed in a smaller envelope and returned to the collecting envelope along with unidentifiable remains. All records were later transferred to a 5-by-8-inch punch card which proved invaluable in cumulating and sorting data (fig. 3). These data were tabulated in monthly periods then grouped into seasons as follows: Winter — January, February, March; Spring

— April, May, June; Summer — July, August, September; and Fall — October, November, December.

The data were evaluated by the occurrence of species only (Scott, 1941; Crabb, 1941; Ferrel et al, 1953). For example, if remains of six sunfish appeared in a scat they were recorded as one occurrence. The percent occurrence was calculated by dividing the number of scats of a period into the number of occurrences of species for the same period.

Reference collections were prepared as follows: Preliminary scat examinations revealed many identifiable objects, especially bones and scales of fishes. Other objects included bones, hair, feathers, teeth, and claws of various vertebrates, and exoskeletal parts of invertebrates. Vertebrates and invertebrates found in and around otter habitat were collected. Fresh specimens of fishes, frogs (*Rana pretiosa*), toads (*Bufo boreas*), snakes (*Thamnophis elegans*), salamanders (*Ambystoma macrodactylum*), and lizards (*Gerrhonotus coeruleus*), were reduced to skeletal remains by boiling in water 3-5 minutes. Scales, pharyngeal teeth, otoliths, and characteristic bones of each species, such as maxillary, opercular, preopercular, dentary, vertebrae and others, were separated and mounted on colored cards (fig. 3). A few mammals were likewise prepared but the availability of the collection at Montana State College made it unnecessary to prepare complete collections.

Reference hair collections were restricted to fur bearers (otter, beaver, muskrat, mink). Only these animals were considered in the study. Reference slides were made of the fur and guard hairs from the neck, chest, back, rump, abdomen, side and tail. Scalation, medulla structure and measurements were used as a basis for comparison with unknowns found in the scats (Mathiak, 1938; Mayer, 1952).

A few breast feathers from representatives of the bird orders found in and around the waters were mounted on cards. Feathers in scats were compared but only those of the Anatidae and grebes were identified. Shaft forms (round, flat, oval), barb concentration at the base with point of departure from shaft and barbule bases were characters used for segregations. All scats and reference collections used in the study are at Montana State College.

RESULTS

The results of the scat analysis are expressed in table 3 by recording the number and percent of the scats in which an item (species) was represented. A scat usually contained more than one of the items reported in the table and therefore none of the percentages total 100%.

For the entire year and for both areas fish remains were identified most frequently, appearing in 1280 (93.2%) of the 1374 scats. Invertebrates were recorded for 566 (41.2%), amphibians 253 (18.4%), mammals 84 (6.1%), birds 71 (5.2%), and reptiles 5 (0.4%). Each of these groups retained the same position in relative importance throughout all seasons except winter when birds replaced mammals in fourth place. Lagler and Ostenson's (1942) summary of early spring food of otters in Michigan, 1940 and 1941, showed stomach (in percent of total volume of food) and intestinal analyses (in average estimated percent of food by bulk) to be: game and pan fishes (32.0 and 15.9), forage fishes (17.6, 22.7), fish remains (3.0, 13.8), frogs and mudpuppies (16.1, 7.5), other vertebrates (25.8, 0.9), insects (0.8, 4.2), and crayfish (4.7, 35.0) respectively.

TABLE 3.—Species identified in 1374 otter scats from the study areas in northwestern Montana.

	Number of Scats				
	Winter 99	Spring 596	Summer 604	Fall 75	Total 1374
INVERTEBRATES	[3]26(26.3)	248(41.6)	267(44.2)	25(33.3)	566(41.2)
Aquatic insects[4]	5(5.1)	117(19.6)	116(19.2)	8(10.7)	241(17.5)
Water bug	3(3.0)	2(0.3)	6(1.0)	1(1.3)	12(0.9)
Aquatic beetle	5(5.1)	71(11.9)	52(8.6)	9(12.0)	137(10.0)
Stone fly nymphs	6(6.1)	27(4.5)	14(2.3)	3(4.0)	50(3.6)
Dragon fly	.....	8(1.3)	10(1.7)	.....	18(1.3)
Dragon fly nymphs	8(8.1)	47(7.9)	52(8.6)	5(6.7)	112(8.2)
Fresh water shrimp	4(4.0)	85(14.3)	54(8.9)	8(10.7)	151(11.0)
Millipede	.....	6(1.0)	3(0.5)	.....	9(0.7)
FISHES	99(100.)	545(91.4)	561(92.9)	75(100.)	1280(93.2)
Trout	29(29.3)	141(23.7)	59(9.8)	25(33.3)	254(18.5)
Sculpin	25(25.3)	122(20.5)	126(20.9)	16(21.3)	289(21.0)
Squawfish	6(6.1)	48(8.1)	53(8.8)	1(1.3)	108(7.9)
Columbia R. chub	21(21.3)	48(8.1)	3(0.5)	5(6.7)	77(5.6)
Sunfish	33(33.3)	281(47.1)	440(72.8)	45(60.0)	799(58.2)
Sucker	59(59.6)	237(39.8)	127(21.0)	34(45.3)	457(33.3)
Whitefish	10(10.1)	27(4.5)	4(0.6)	11(14.7)	51(3.8)
Bass	4(4.0)	30(5.0)	35(5.8)	.....	69(5.0)
Perch	7(7.1)	36(6.0)	28(4.6)	4(5.3)	75(5.5)
Shiner	14(14.1)	75(12.6)	14(2.3)	13(17.3)	116(8.4)
AMPHIBIANS	9(9.1)	117(19.6)	118(19.5)	9(12.0)	253(18.4)
Frog	9(9.1)	117(19.6)	116(19.2)	8(10.7)	250(18.2)
Salamander	.....	2(0.3)	4(0.7)	1(1.3)	7(0.5)
REPTILES	.....	1(0.2)	4(0.7)	.....	5(0.4)
Snake	.....	1(0.2)	4(0.7)	.....	5(0.4)
BIRDS	5(5.1)	40(6.7)	25(4.1)	1(1.3)	71(5.2)
Unknown	1(1.0)	19(3.2)	9(1.5)	.....	29(2.1)
Duck	4(4.0)	13(2.2)	14(2.3)	1(1.3)	32(2.3)
Grebe	.....	8(1.3)	2(0.2)	.....	10(0.7)
MAMMALS	2(2.0)	48(8.1)	32(5.3)	2(2.7)	84(6.1)
Unknown	1(1.0)	3(0.5)	3(0.5)	.....	7(0.5)
Otter (trace)[5]	6(6.1)	42(7.0)	72(11.9)	10(13.3)	130(9.5)
Beaver	1(1.0)	7(1.2)	1(0.2)	1(1.3)	10(0.7)
Muskrat	.....	33(5.5)	27(4.5)	1(1.3)	61(4.4)
Meadow mouse	.....	2(0.3)	.....	.....	2(0.1)
Shrew	.....	1(0.2)	.....	.....	1(0.1)
Mink	.....	1(0.2)	1(0.2)	.....	2(0.1)
Ground squirrel	.....	1(0.2)	.....	.....	1(0.1)

[3] First figure is the number of scats the item appeared within. The figure in brackets is the percentage of scats the item appeared within.

[4] Undetermined exoskeletal fragments of aquatic insects.

[5] Not included for analysis.

Of the fish, sunfish occurred most frequently, 58.2% of all scats. It was most frequent in summer scats; 72.8% of the 604 assigned to that season. It was the most commonly represented fish during all seasons except winter when it was surpassed by the sucker. Suckers ranked second (33.3%). They were most prominent in winter (59.6%) and fall (45.3%). The fish third in importance was the sculpin which occurred in 21% of all scats and was uniformly represented throughout the four seasons.. All of the above fishes occurred in 20% or more of the scats for each of the seasons. Trout were fourth in occurrence (18.5%) but showed low representation in summer (9.8%) and high in fall (33.3%). Other fish represented occurred in less than 10% of the droppings. In order of occurrence, they were: shiner, squawfish, Columbia River chub, perch, bass and whitefish (table 3).

Many scats contained small insect remains that could have been in the alimentary canals of fish taken by otter. Lagler and Otsenson (1942) concluded this in their study of otter stomachs and intestinal tracts. The larger insects represented in the scats were considered as a food taken directly by the otter.

Invertebrates considered as food were in 566 or 41.2% of the 1374 scats. The category "aquatic insects" (17.5%) appeared to be mostly fragments of dragon fly nymphs (Odonata) (table 3). If this assumption is correct, then dragon fly nymphs (8.2% plus "aquatic insects" 17.5%) occurred most frequently in the group followed by fresh water shrimp (*Gammarus*) (11.0%) and aquatic beetles (Coleoptera) (10.0%). The greatest occurrence of invertebrates appeared in spring (41.6%) and summer (44.2%). The representation for the winter and fall was 26.3 and 33.3% respectively.

Frog remains appeared in 250 or 18.2% of the droppings. The spring and summer representation was 19.6 and 19.2% respectively. They were in 9.1 and 10.7% of winter and fall scats. Salamanders were represented by a trace in all periods except winter.

Mammal remains and/or hair were found in 84 or 6.1% of the total. Periodic differences showed the winter to be lowest (2.0%) with the other seasons ranging from 2.7 to 8.1%. One hundred thirty (9.5%) droppings contained a trace of otter hair. A trace was considered as such if it were possible to make 3 or more examination slides from the material. Otter hair was never found in greater quantity than an 1/8 inch tuft suggesting it was taken while the otter was grooming itself. Fisher (1940) and Murie (1940) have observed the sea otter (*Enhydra lutris*) spending much time cleaning itself and its young.

Muskrat was identified in 61 (4.4%) of the scats. The occurrence was concentrated in spring 33 (5.5%) and summer 27 (4.5%), absent in winter and in one scat for the fall period. Beaver was in 10 (0.7%) with greatest occurrence 7 (1.2%) in the spring and showing in one scat for each of the other three seasons. Mink, meadow mouse (*Microtus*), shrew (*Sorex*), and ground squirrel (*Citellus*) were also identified.

Of the 71 (5.2%) scats containing feathers, 29 were undetermined, 32 (2.3%) had duck and 10 (0.7%) contained grebe feathers. Feathers appeared in 40 (6.7%) scats from the spring collection, 25 (4.1%) from the summer, 5 (5.1%) in winter and 1 (1.3%) in fall.

The Michigan study of Lagler and Ostenson (1942) revealed a limited occurrence of one mammal and two birds to be of too few data to suggest

these to be staples in the food of the otter. This study, revealing occurrence of 71 scats containing feathers and 84 with mammals, indicated that the otter fed upon these animals commonly.

Snakes occurred in 5 (0.4%) of the total. Four (0.7%) of these were summer scats.

By comparing the remains of characteristic bones (table 1) in scats with reference collections it was possible to determine the approximate size of the fish eaten. Remains indicated 14-inch trout and 16-inch suckers were frequently taken. Lagler and Ostenson (1942) report trout in the diet of otters to average 4½ inches, suckers 5 inches.

No "leavings" or "caches" of fishes were found to have been left by the otter. All catches seem to be completely utilized.

Western painted turtles (*Chrysemys picta*) were abundant in the area but none appeared in any scat. An otter was observed sniffing a turtle which was on a log in the water without disturbing it.

On one occasion a golden eye duck (*Bucephala*) wing tip and a few feathers were found with otter "sign" close by. During December, a mutilated frog was found on the ice next to a beaver house which showed recent otter activity, tracks and "sign."

Comparison of Thompson and Gary areas.—The droppings from the Thompson area contained the same categories of animals and in the same order of frequency as the complete scat collection (tables 3 and 4). Those found in 1122 droppings were: Fish 1093 (97.4%), invertebrates 376 (33.5%), amphibians 137 (12.2%), birds 43 (3.8%), mammals 22 (2.0%) and reptiles 4 (0.4%) For Gary's lake, invertebrates 190 (75.4%), barely take the number one occurrence from the fishes, 187 (74.2%). The same relations continue for the other groups except for mammals preceding birds: Amphibians 116 (46.0%), mammals 62 (24.6%), birds 28 (11.1%) and reptiles 1 (0.4%) for 252 scats.

At Gary's, the fish occurring in the highest percentage of the scats was the trout 131 (52.0%). Trout appeared mostly in winter (66.7%) and fall (100%), least in the summer (38.6%). On Thompson area, trout ranked fourth and maintained the same seasonal trend found at the other study area, i.e., highest in winter (24.1%) and fall (23.1%), lowest in summer (6.0%). The ranking fish at the Thompson area was sunfish 798 (71.1%) with a high in summer (82.4%) and low in winter (37.9%). This fish was not collected or reported to occur in Gary's Lake. Suckers were second in occurrence for both Thompson 349 (31.1%) and Gary's 108 (42.9%). They showed the same seasonal trend for the respective areas; high in winter (56.3 and 83.3%) and low for the summer (21.0 and 21.4%). Third place for Gary's was the sculpin, occurring in 78 (31.0%) and showing greatest for summer (42.9%) and fall (50.0%). At Thompson the third important fish was also the sculpin 211 (18.8%). It showed about equal relations throughout the spring (18.8%), summer (18.0%) and fall (17.0%) but increased in winter (25.3%). The fish occurring fourth at Gary's was the shiner 63 (25.0%). These were present in at least 30% of the scats for the winter, spring and fall with lowest representation during the summer (7.1%). This low trend for shiner also appears for the same period in the Thompson area (1.7%) although its occurrence at no season approached that at Gary's. Squawfish, bass and perch were entirely absent from any analyzed scats collected from Gary's area

TABLE 4.—A comparison of the species identified in otter scats from Thompson area with those from Gary's Lake.

	Number of scats				
	THOMPSON AREA				
	Winter 87	Spring 436	Summer 534	Fall 65	Total 1122
INVERTEBRATES	18(20.7)	134(30.7)	208(39.0)	16(24.6)	376(33.5)
Aquatic insects	3(3.4)	60(13.8)	102(19.1)	5(7.8)	170(15.2)
Water bug	3(3.4)	.....	5(0.9)	1(1.5)	9(0.8)
Aquatic beetle	3(3.4)	23(5.3)	29(5.4)	4(6.2)	59(5.3)
Stone fly nymphs	6(6.9)	24(5.5)	14(2.6)	3(4.6)	47(4.2)
Dragon fly	.....	2(0.5)	7(1.3)	.....	9(0.8)
Dragon fly nymphs	5(5.7)	18(4.1)	38(7.1)	3(4.6)	64(5.7)
Fresh water shrimp	1(1.1)	23(5.3)	31(5.8)	2(3.1)	57(5.1)
Millipede	.....	6(1.4)	3(0.6)	.....	9(0.8)
FISHES	87(100.)	427(97.9)	514(96.3)	65(100.)	1093(97.4)
Trout	21(24.1)	55(12.6)	32(6.0)	15(23.1)	123(11.0)
Sculpin	22(25.3)	82(18.8)	96(18.0)	11(17.0)	211(18.8)
Squawfish	6(6.9)	48(11.0)	53(9.9)	1(1.5)	108(9.6)
Columbia R. chub	21(24.1)	46(10.6)	3(0.6)	5(7.7)	75(6.7)
Sunfish	33(37.9)	280(64.2)	440(82.4)	45(69.2)	798(71.1)
Sucker	49(56.3)	163(37.4)	112(21.0)	25(38.5)	349(31.1)
Whitefish	9(10.3)	22(5.0)	4(0.7)	10(15.4)	45(4.0)
Bass	4(4.6)	30(6.9)	35(6.6)	.....	69(6.1)
Perch	7(8.0)	36(8.3)	28(5.2)	4(6.2)	75(6.7)
Shiner	10(11.5)	24(5.5)	9(1.7)	10(15.4)	53(4.7)
AMPHIBIANS	5(5.7)	42(9.6)	86(16.1)	4(6.2)	137(12.2)
Frog	5(5.7)	42(9.6)	84(15.7)	3(4.6)	134(11.9)
Salamander	.....	.....	4(0.7)	1(1.5)	5(0.4)
REPTILES	.....	.....	4(0.7)	.....	4(0.4)
Snake	.....	.....	4(0.7)	.....	4(0.4)
BIRDS	3(3.4)	17(3.9)	22(4.1)	1(1.5)	43(3.8)
Unknown	.....	7(1.6)	9(1.7)	.....	16(1.4)
Duck	3(3.4)	7(1.6)	11(2.1)	1(1.5)	22(2.0)
Grebe	.....	3(0.7)	2(0.4)	.....	5(0.4)
MAMMALS	1(1.1)	5(1.1)	15(2.8)	1(1.5)	22(2.0)
Unknown	.....	1(0.2)	3(0.6)	.....	4(0.4)
Otter (trace)	5(5.7)	31(7.1)	50(9.4)	9(13.8)	95(8.5)
Beaver	1(1.1)	.....	.....	1(1.5)	2(0.2)
Muskrat	.....	3(0.7)	11(2.1)	.....	14(1.2)
Meadow Mouse	.....	.....	.....	.....	.....
Shrew	.....	.....	.....	.....	.....
Mink	.....	.....	1(0.2)	.....	1(0.1)
Ground squirrel	.....	1(0.2)	.....	.....	1(0.1)

Number of scats

GARY'S LAKE

	Winter 12	Spring 160	Summer 70	Fall 10	Total 252
INVERTEBRATES	8(66.6)	114(71.3)	59(84.3)	9(90.0)	190(75.4)
Aquatic insects	2(16.7)	41(25.6)	25(35.7)	3(30.0)	71(28.2)
Water bug	.....	2(1.3)	1(1.4)	.....	3(1.2)
Aquatic beetle	2(16.7)	48(30.0)	23(32.9)	5(50.0)	78(31.0)
Stone fly nymphs	.....	3(1.9)	.....	.....	3(1.2)
Dragon fly	.....	6(3.8)	3(4.3)	.....	9(3.6)
Dragon fly nymphs	3(25.0)	29(18.1)	14(20.0)	2(20.0)	48(19.0)
Fresh water shrimp	3(25.0)	62(38.8)	23(32.9)	6(60.0)	94(37.3)
Millipede	.....	.....	.....	.....	.....
FISHES	12(100.)	118(73.8)	47(67.1)	10(100.)	187(74.2)
Trout	8(66.6)	86(53.8)	27(38.6)	10(100.)	131(52.0)
Sculpin	3(25.0)	40(25.0)	30(42.9)	5(50.0)	78(31.0)
Squawfish	.....	.....	.....	.....	.....
Columbia R. chub	.....	2(1.3)	.....	.....	2(0.8)
Sunfish	.....	1(0.6)	.....	.....	1(0.4)
Sucker	10(83.3)	74(46.3)	15(21.4)	9(90.0)	108(42.9)
Whitefish	1(8.3)	5(3.1)	.....	1(10.0)	7(2.8)
Bass	.....	.....	.....	.....	.....
Perch	.....	.....	.....	.....	.....
Shiner	4(33.3)	51(31.9)	5(7.1)	3(30.0)	63(25.0)
AMPHIBIANS	4(33.3)	75(46.0)	32(45.7)	5(50.0)	116(46.0)
Frog	4(33.3)	75(46.0)	32(45.7)	5(50.0)	116(46.0)
Salamanders	.....	2(1.3)	.....	.....	2(0.8)
REPTILES	.....	1(0.6)	.....	.....	1(0.4)
Snake	.....	1(0.6)	.....	.....	1(0.4)
BIRDS	2(16.6)	23(14.4)	3(4.3)	.....	28(11.1)
Unknown	1(8.3)	12(7.5)	.....	.....	13(5.2)
Duck	1(8.3)	6(3.8)	3(4.3)	.....	10(4.0)
Grebe	.....	5(3.1)	.....	.....	5(2.0)
MAMMALS	1(8.3)	43(26.3)	17(24.3)	1(10.0)	62(24.6)
Unknown	1(8.3)	2(1.3)	.....	.....	3(1.2)
Otter (trace)	1(8.3)	11(6.9)	22(31.4)	1(10.0)	35(13.9)
Beaver	.....	7(4.4)	1(1.4)	.....	8(3.2)
Muskrat	.....	30(18.8)	16(22.9)	1(10.0)	47(18.7)
Meadow Mouse	.....	2(1.3)	.....	.....	2(0.8)
Shrew	.....	1(0.6)	.....	.....	1(0.4)
Mink	.....	1(0.6)	.....	.....	1(0.4)
Ground Squirrel	.....	.....	.....	.....	.....

and the only occurrence for a Columbia River chub in 2 scats and sunfish in 1 were recorded for the spring. Evidence suggests these were picked up elsewhere. For Thompson, the squawfish had a total occurrence of 108 (9.6%). It was greatest for spring 48 (11.0%) and summer 53 (9.9%); lowest for fall 1 (1.5%). Columbia River chub totaled 75 (6.7%); of these 21 (24.1%) were in the winter, 46 (10.6%) in spring and 3 (0.6%) in summer. Of all appearances of bass 69 (6.1%), spring 30 (6.9%) and summer 35 (6.6%) were most prominent followed by 4 (4.6%) for winter and entirely absent during the fall. Perch were found in 75 (6.7%) scats; seasonal usage ranged from 5.2 to 8.3%. Total whitefish occurrence was 45 (4.0%). These appeared mostly in the fall 10 (15.4%) and winter 9 (10.3%) followed by spring 22 (5.0%) and then summer 4 (0.7%). This same trend appeared for Gary's Lake but too few data are available for definite conclusions. Only 7 (2.8%) appeared, with fall 1 (10.0%) and winter 1 (8.3%) highest, followed by spring 5 (3.1%) and none for summer.

Invertebrates are 2 to 3 times greater in percent occurrence at Gary's than at Thompson area for all seasons but no season had less than 20% for either area. The most prominent at Gary's were: fresh water shrimp 94 (37.3%), aquatic beetles 78 (31.0%), "aquatic insects" 71 (28.2%) and dragon fly nymphs 48 (19.0%). At Thompson area "aquatic insects" were present in 170 (15.2%) of the total; all others were represented less than 6% each. Stonefiy nymphs (Plecoptera) were represented in all seasons at Thompson but only during the spring at Gary's.

Frogs appeared in 46.0% of the collection at Gary's and were recorded for 33.3% or more for all seasons. The Thompson occurrence was 11.9% showing highest for summer 15.7% and lowest in fall 4.6%. Salamanders were taken as a trace in both areas.

Hair and mammal remains were in 96 (38.1%) scats at Gary's and 116 (10.3%) at Thompson. Excluding traces of otter hair the figures are 62 (24.6%) and 22 (2.0%). Muskrat was the most numerous in scats containing hair found in both areas. Of the total 47 (18.7%) containing muskrat hair at Gary's, 30 (18.8%) were in the spring, 16 (22.9%) in summer, 1 (10.0%) in fall and absent for winter. The Thompson area scats with muskrat hair 14 (1.2%), was highest for summer 11 (2.1%) followed by spring 3 (0.7%) and absent in both winter and fall.

Beaver occurrence was 8 (3.2%) for Gary's and only 2 (0.2%) for the Thompson area. All usage at Gary's was in spring 7 (4.4%) except 1 (1.4%) in summer. At Thompson it was recorded in 1 scat each for winter and fall. Usage of other mammals for both areas was too insignificant for comparison (table 2).

Of the 28 (11.1%) scats from Gary's having feathers, 23 (14.4%) occurred in the spring, 3 (4.3%) in summer and 2 (16.6%) in winter. Thirteen (5.2%) were of unknown identity, 10 (4.0%) were duck and 5 (2.0%) grebes. All grebes were recorded for the spring period. Duck appeared in 6 (3.8%) spring scats, 3 (4.3%) in summer, 1 (8.3%) in winter and none in fall. Spring 17 (3.9%) and summer 22 (4.1%) shared about equal importance for feather occurrence recorded for Thompson area. From this area 16 (1.4%) were classified as unknown for the total 43 (3.8%). Twenty-two (2.0%) were duck and 5 (0.4%) grebes. Ducks appeared in 11 (2.1%) scats during the summer, 7 (1.6%) in spring, 3 (3.4%) in winter and 1 (1.5%)

in fall. Grebes were recorded for spring 3 (0.7%) and summer 2 (0.4%). The incidence of feather occurrence was greatest during June at Gary's, whereas it was highest during August at Thompson area.

Reptiles appeared in 4 (0.7%) scats, all from summer collections at Thompson and 1 (0.6%) for the spring at Gary's.

Tapeworm incidence.—Tapeworm proglottids occurred in scats from both areas. They were in 12 (8.6%) of the April scats with 11 (16.2%) for Thompson and 1 (1.4%) for Gary's; 17 (9.7%) for May, 17 (11.6%) and zero; 17 (6.1%) for June, 16 (7.2%) and 1 (1.7%); 14 (5.7%) for July, 11 (5.1%) and 3 (9.1%2; 20 (7.2%) for August, 20 (7.8%) and zero. Scats contained from 2 to 76 proglottids which ranged from 1/8 to 1½ inches. A collection of 20 squawfish from the Pleasant Valley River, adjacent to an often used otter latrine, revealed 8 to contain tapeworm larvae. These were found to a lesser extent in shiner and perch. The proglottids and larval stages were both identified as *Ligula intestinalis* by the Agricultural Research Center, Beltsville, Maryland. Wardle (1935) mentions this tapeworm as frequent in fish-eating birds.

DISCUSSION

The data indicate that the food of the otter varies within restricted limits from one area to another. The reasons for these differences are not readily interpreted. In some cases it seems to be a case of availability of prey (numbers) but in others this is not readily apparent. It seems obvious that the habits of certain fishes would make them more vulnerable than others irrespective of total populations. It follows that the limited sampling of fish populations by gill netting, electric shocking, and fishing did not necessarily indicate the relative abundance of vulnerable populations. The predominant fish, sunfish (71.1% of scats from Thompson), eaten by the otter was not taken in any great numbers by sampling. It was noted while walking the lake shores that sunfish were abundant close to the water's edge during the spring and summer seasons. Selective angling in a few of these places did increase the sunfish catch but still not in proportion to their occurrence in scats. In all probability the habits of the sunfish, during at least some periods, make them more available to the otter. One observation of two otter in a small lake showed their manner of "hunting" to be that of circling the lake rather close to the shore line. On the other hand, the high incidence of sunfish in the scats at Thompson could possibly indicate a preference for this species but at Gary's where sunfish were absent otter were equally abundant and diverted their attention towards other prey.

The populations of bass, trout and shiner as indicated by sampling were also lower than is suggested by their occurrence in scats.

In contrast to the fishes above, the squawfish and Columbia River chub did not occur as frequently in scats as their apparent abundance indicated by fishing in pools adjacent to often used latrines would suggest. One catch for 30 minutes of fishing yielded 20 squawfish. At a lake near otter latrines, 3 hours of fishing resulted in a catch of over 100 squawfish. These fishes were only represented in 16.3% of the total scats.

Whitefish were taken in deep water gill net sets and in greater proportion than their incidence in droppings. Scheffer (1953) reported the capture of otter (*Lutra canadensis*) in crab pots set in 60 feet of water. Numbers of perch caught by fishing and gill nets gave an indication of greater occurrence than scat analysis. From 52 scats collected on the lower Thompson Lake, 21 had

perch remains (40.4%) and 16 (30.8%) had sunfish. In the upper Thompson Lake, perch were in 21 of 226 scats (9.3%) and sunfish in 205 scats (90.7%). The reasons for the increase of perch in the diet from one end of these lakes to the other is difficult to evaluate.

In some instances there does appear to be a direct correlation between relative abundance and utilization. The catch of sculpins by shocking seemed proportionate to the occurrence in scats as did the numbers of suckers caught in gill nets (table 1).

Otter predation on fur bearers seemed to be in relation to availability. Gary's Lake had a higher incidence of beaver and muskrat than Thompson (table 2) and the degree of utilization was higher. Muskrat remains first appeared in the scats deposited during April for both areas. At Gary's, scats with muskrat reached a peak in June, occurring in 14. Evidence of muskrat was highest during August at Thompson area, appearing in 5 scats. The predominant occurrence of muskrat remains in the spring and summer suggest the vulnerability of this species when their numbers exceed the security levels under prevailing conditions (Errington, 1943 and 1946).

Of the 8 scats containing beaver at Gary's, 5 occurred during April, 2 in May and 1 for August. The two for Thompson's consisted of one each for fall and winter.

SUMMARY

A food habits study by scat analysis was conducted in the Thompson lakes region of Lincoln County, Montana, to help evaluate the economic status of the otter.

Otter latrines were located by walking the shore lines of lakes and streams; 96 were discovered on fallen trees, beaver houses and the shore.

Otter scats were easily distinguished by size, shape, and odor. A total of 2209 were collected between April, 1952, and May, 1953. Approximate date of deposit was determined for 1374 which were assigned to winter, spring, summer and fall. These constituted the basis for this study.

The limited use of electric shocking, gill net sets and fishing were employed in an attempt to obtain the relative abundance of fishes in the various waters. An indication of fur bearer abundance was afforded by "sign".

Scats were analyzed in a dry state. Each was broken apart in a culture dish with dissecting needle and tweezer. The complete scat was searched for identifiable remains of items in the diet. These were identified by comparisons with reference collections. Hair identifications were restricted to fur bearers (otter, beaver, muskrat, mink); feathers to Anatidae and grebes. All scats and reference collections are at Montana State College.

Data are expressed at percent occurrence by seasons which was calculated by dividing the number of scats for a season into the number of occurrences of an item.

Data for two separated areas (Thompson and Gary) are compared.

For the entire year and for both areas fish remains were identified most frequently, appearing in 1280 (93.2%) of the scats. Invertebrates were recorded for 566 (41.2%), amphibians 253 (18.4%), mammals 84 (6.1%), birds 71 (5.2%) and reptiles 5 (0.4%).

Considering all scats, sunfish occurred in 58.2%, sucker 33.3%, sculpin 21.0%, and trout 18.5%. This same order of importance was established for

the Thompson area. Gary's Lake was: trout 52.0%, sucker 42.9%, sculpin 31.0% and shiner 25.0%.

Dragon fly nymphs, aquatic beetles and fresh water shrimp appeared in scats consistently but seldom made up an appreciable percent of the scat. It was most common to find 1-5 of these in a dropping.

Frogs were found to be a prominent part of the diet and were found throughout all seasons.

Muskrat occurred in 4.4% of total scats but was present in 18.7% of the collection at Gary's lake and predominant during spring and summer. The highest incidence was in June, occurring in 14 scats. Beaver appeared in 10 or 0.7% of all scats with 8 occurring at Gary's and 2 for the Thompson.

The data suggest availability to be important in determining the food habits of the otter.

Tapeworm proglottids, *Ligula intestinalis*, were found in scats from both areas.

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Inter- and Intraspecific Variation in Oregon Frogs of the Genus Rana

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The frogs of the genus *Rana* have presented a difficult taxonomic and distributional problem to herpetologists working in central Oregon. Four native species, one of which includes two subspecies, have been recorded from the area. These are *R. a. aurora, R. cascadae, R. p. pretiosa, R. p. luteiventris,* and *R. b. boylii.* Confusion has developed in distinguishing between *R. aurora, R. p. pretiosa, R. p. luteiventris,* and *R. cascadae,* but *R. b. boylii* has, to my knowledge, been confused with no other form in this area. This paper deals with the first four forms.

This study is limited to the state of Oregon. Most of the collecting was carried out in an area roughly from the summit of the Coast Range, east to Mill Creek in Crook County, a distance of some 140 miles, and from State Highway 222 south to State Highway 58, a distance of about 80 miles. This area contains part of the Coast Range, the Willamette Valley, the central Oregon Cascades, and a small area east of the Cascades. It contains within its limits, therefore, portions of the known ranges of all the forms in this study.

Acknowledgments.—I am deeply indebted to Dr. Robert M. Storm of Oregon State College for both assistance and encouragement in the preparation of this paper. Not only did he suggest the problem and provide much helpful advice, but he also provided the photographs used. I also wish to express my gratitude to the many others at Oregon State who have contributed ideas and information in the behalf of this work.

Taxonomic status.—*R. aurora* was first described from the Puget Sound area in 1852 by Baird and Girard, and has been recognized from that time to the present. *R. pretiosa* was described the following year from the same locality by the same authors, 1853. It likewise has been considered a valid species. *R. p. luteiventris* was described by Thompson (1913) and is still recognized by Stebbins (1951). Slevin, 1928, did not consider it to be distinct from *R. pretiosa. R. cascadae* was described by Slater (1939) from the Elysian Fields, Mount Rainier National Park, Washington. It is considered by Stebbins (1951) to be a subspecies of *R. aurora.*

Diagnostic characters.—*R. pretiosa* may be distinguished from the other two species by its shorter legs, greater amount of webbing, lack of mottling on the sides, lack of mask, and presumably by the greater roughness of its skin.

R. p. luteiventris may be distinguished from *R. p. pretiosa* by the difference in coloration and by the foot tubercles. The bright color on the ventral surface is orange-yellow in adult *R. p. luteiventris,* and bright salmon-red in adult *R. p. pretiosa. R. p. luteiventris,* furthermore, lacks the tubercle at the base of the fourth toe, which is characteristic of *R. p. pretiosa.*

R. aurora may be distinguished from *R. cascadae* by the red color on the ventral surface of *R. aurora* as opposed to the yellowish ventral surface of *R. cascadae,* by the red, yellow and green with heavy mottling in the groin of *R. aurora* compared with the yellowish, lightly mottled groin of *R. cascadae,*

and the greater stoutness of the toes and greater roughness of the skin in *R. cascadae*.

Two main problems will be taken into consideration on the following pages. First, the distribution of the three forms, excluding the subspecies, and second, the status and relationships of the three or four forms within the area studied.

DISTRIBUTION

Records from the literature.—Gordon (1939) states that *R. aurora* is probably distributed over most of Oregon west of the Cascades and lists localities as shown in fig. 1. He also records *R. p. pretiosa* from western Oregon and *R. p. luteiventris* from the Cascades and eastward as indicated on the map.

Evenden (1943) reports *R. p. luteiventris* from Santiam, Red Butte, Jorn, Bowerman, and Blue lakes in the Cascades, and states that at Jorn Lake it is found with *R. p. pretiosa*.

So far as I can find, *R. cascadae* has been recorded from Oregon in three publications. Wright and Wright (1949) state that Slater has a number from Breitenbush Lake, Marion County. Dunlap and Storm (1951) record it from the rest of the areas of literature records on the map (fig. 1). Stebbins (1951) also mentions it as being found in the Cascades.

Gordon (1939) states that "specimens of *R. p. luteiventris* from the high Cascades and eastern Oregon are paler and tend toward yellowish rather than reddish in ventral coloration". Since the collecting recorded by Gordon was done prior to 1939 (when *R. cascadae* was described), it would appear that any yellow or orange-legged frog in the region was considered by him to be *R. p. luteiventris*. Many of the earlier reports of *R. p. luteiventris* from the Cascades of Oregon are referable to *R. cascadae*.

After collecting in the Jorn Lake area, I am forced to conclude that Evenden's report of *R. pretiosa* in that lake is based on erroneous identification of *R. cascadae*.

Specimens Examined.—In addition to those reported by Dunlap and Storm I have collected living frogs or examined preserved material that best fit the *R. cascadae* diagnosis from the following localities: LANE: (Benson Lake, 5300 ft.; Irish Camp Lake, 4600 ft.; Coffee Lake, 4950 ft.; Fingerboard Prairie, 4050 ft.; Frog Camp Forest Camp, 4800 ft.; Hunts Cove, 5400 ft.); LINN: (Lost Lake Creek, 4300 ft.; Fay Lake, 4000 ft.; Big Meadows Forest Camp, 3600 ft.; Duffy Lake, 4650 ft.; Toad Creek, 3300 ft.; Marion Creek, 2950 ft.); DESCHUTES: (Corral Swamps, 5050 ft.; Lemish Lake, 5150 ft., Big Cultus Lake, 4750 ft., Elk Lake, 4890 ft., Davis Lake Trail, 4900-5000 ft., Green Lakes, 6500 ft., Three Creeks Lake, 6400 ft., West Lava Forest Camp, 5200 ft.); JEFFERSON: (Link Creek, 3450 ft.).

Specimens of *R. aurora* from the following counties have been examined: MULTNOMAH (Portland, 35 ft.); BENTON (McFadden's Marsh, twelve miles south of Corvallis, 250 ft., Coffin Butte, 400 ft., five miles up Woods Creek Road, 700 ft., Summit, 730 ft., Blodgett, 630 ft., Alsea Fish Hatchery, 300 ft., three miles south Corvallis, 250 ft.); LINN (three miles southeast Stayton, 400 ft., three miles southeast Corvallis, 230 ft., Owl Creek, 225 ft., R4W T11S Sec. 34, 225 ft., Wiley Creek, three miles south Foster, 700 ft., one and one half miles up Bear Pass Road, 1300 ft., three-quarters mile above Pamelia Creek Junction, 2300 ft., little Stream one mile south Marion Forks, 2600 ft.); LANE (McKenzie Bridge, 1500 ft., Lost Creek at Limberlost Forest Camp, 1740 ft., Salt Creek, two miles southeast McCredie Springs, 2100 ft., five miles northwest Salt Creek Falls, 2300 ft., Salt Creek Falls, 3800 ft., Siltcoos Forest Camp, 50 ft.); DOUGLAS (two miles

south Douglas-Lane County line, 50 ft.); LINCOLN (Yaquina); COOS (Charleston, 30 ft.); CURRY (Pistol River).

Specimens assigned to *R. pretiosa* have been examined from the following county localities: MULTNOMAH (Portland, 40 ft.); BENTON (McFaddens Marsh, twelve miles south of Corvallis, 250 ft.); LINN (R4W T11S Sec. 34, 225 ft.); DESCHUTES (Big Cultus Lake, 4750 ft., Little Cultus Lake, 4850 ft., Mud Lake, 4800 ft., Deschutes River, R11E T19S Sec. 4, 4100 ft., Little Deschutes River, 4220 ft., between Lapine and Little Deschutes River, 4230 ft., Cultus Creek, 4500 ft., Big Lava Lake, 4740 ft.); CROOK (Mill Creek, ten miles east Prinville, 3100 ft.); KLAMATH (Crater Lake, 6000 ft., Davis Lake, 4395 ft., Odell Creek, 4458 ft.); GRANT (Hotsprings, ten miles south of John Day, 4100 ft., Middle Fork John Day River approximately 3000 ft.); HARNEY (Camp Creek, one quarter mile north Malheur Cave, Fish Lake, Steens Mts.); UNION; WALLOWA (Forks Meadows).

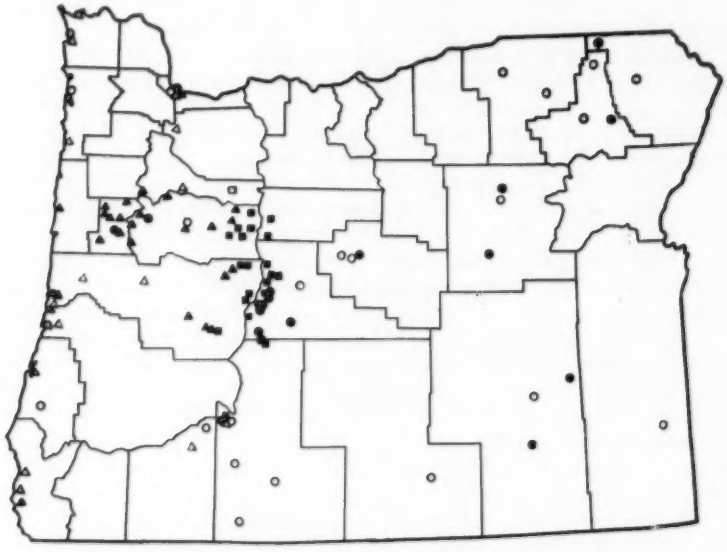

FIG. 1.—Map of Oregon showing locality records. Solid symbols represent specimens examined by the author. Hollow symbols represent literature records accepted by the author. ▲ *R. aurora;* ■ *R. cascadae;* ● *R. pretiosa.*

From the above localities and fig. 1 it may be seen that *R. cascadae* is found from 2900 ft. at Jack Creek, Jefferson County to at least 6500 ft. (Green Lakes, Deschutes County) in the Cascade Mountains and their foothills. Its range overlaps that of *R. aurora* on the west in the vicinity of Salt Creek Falls, and the ranges of the two forms approach each other on the North Santiam River and the McKenzie River. *R. cascadae* and *R. pretiosa* overlap in distribution at Odell Creek and Crater Lake in Klamath County and at Big Cultus Lake in Deschutes County.

R. aurora ranges west of the Cascades from near sealevel to at least an altitude of 3800 ft. at Salt Creek Falls. It is rather scattered above 2000 ft.

R. pretiosa was found west of the Cascades from an altitude of 50 ft. to

at least 264 ft. East of the Cascades it is found from an altitude of approximately 3000 ft. to about 4850 ft. at Little Cultus Lake and near 6000 ft. at Crater Lake.

METHODS AND DATA

Slater (1939) states that "some previous collectors have placed specimens of this species (*R. cascadae*) with *R. aurora* while others have called them *R. pretiosa*. . .". As mentioned earlier, Stebbins (1951) considers it to be a subspecies of *R. aurora*. Most of the remaining part of the paper will be used in an attempt to determine the relationships of these frogs in Oregon.

Statistical Analysis.—The objective of this analysis is an attempt to find characters that differ among the three species of frogs and, of equal interest, those characters that remain constant throughout the several species. By finding what characters the groups have or do not have in common, conclusions as to their relationships to one another may be drawn. While the idea does have certain defects, we may say with reservations, that those forms having the most characters in common are the more closely related. All *R. pretiosa* material is lumped in this study.

Material and Methods

A series of fourteen measurements was taken on twenty adult frogs of each sex for each species, one hundred twenty frogs in all. All measurements were taken on preserved frogs by use of venier calipers which were read to the nearest one-tenth millimeter. The following measurements were taken: 1) snout-anus length, measured from the tip of the snout in a straight line to the anal opening; 2) head length, measured from the tip of the snout in a straight line to the posterior edge of the tympanum; 3) head width, taken across the jaw at the tympanum; 4) diameter of eye, from the anterior corner of the eyelid to the posterior corner; 5) diameter of tympanum, from its anterior to its posterior rim; 6) internasal space, from the inner side of one nares to the inner side of the other; 7) interocular space, from the medial base of one bulbus to that of the other; 8) distance from the anterior margin of the eye to the tip of the snout; 9) anterior margin of eye to the nares; 10) length of femur, distance from anus to the end of the flexed knee joint with the thigh perpendicular to the longitudinal axis of the body; 11) length of tibia, distance from the knee point to the flexed tibio- tarsal joint; 12) length of tarsus, distance from the flexed tibio-tarsal joint to the tarso-metatarsal joint; 13) length of foot, distance from the flexed tibio-tarsal joint to the tip of the fourth toe; 14) length of fourth toe, distance from flexed tarso-metatarsal joint to the tip of the fourth toe.

The measurements of the eye and tympanum diameter, interocular, internasal, anterior margin of eye to tip of snout, and anterior margin of eye to nares were all taken under a binocular microscope.

For purposes of comparison of individuals and species all measurements have been reduced to ratios. The use of these ratios rests on the assumption that the various body structures grow in direct proportion to each other. In the case of adult animals this assumption is apparently correct enough to

enable the ratios to be of value. (Moore, 1944). The values of these ratios were obtained by dividing the smaller measurement by the larger one and multiplying by one hundred.

The following fourteen ratios are used in the study: head width/snout-anus length; head length/snout-anus length; head length/head width; diameter of tympanum/diameter of eye; interocular space/internasal space; internasal space/head width; anter margin of eye to nares/anterior margin of eye to tip of snout; length femur/snout-anus length; length femur/length tibia; length tarsus/length femur; length femur/length foot; length tibia/snout-anus length; length tarsus/length foot; length fourth toe/length foot.

The method of statistical analysis used is a 2 x 3 completely randomized factorial design with equal numbers of observations. This is a type of analysis of variance, so it is based on the F distribution.

In this design there are two factors used, one with two levels of one factor (sex) and the other with three levels (species). The species are set up into three columns (one for each species), each of which contains twenty observations of the same ratio for males and twenty for females. Thus, each of the

TABLE 1.—Showing F values and critical regions for species, sex and interation for each ration. Degrees of freedom; error mean square-114, interaction-2, sex-1, species-2.

		VARIATION DUE TO:				
		Species	Sex	Interaction	Error	Pooled
		Critical Region				
Ratio		$F > 4.80$	$F > 6.86$	$F > 4.81$		
Head width/	Mean sq.	6.638	0.919	8.094	2.760	2.852
snout-anus	F	2.33	0.30	2.93		
Head length/	Mean sq.	31.793	30.091	1.593	2.454	2.439
snout-anus	F	13.03*	12.33*	0.63		
Head length/	Mean sq.	107.220	353.983	32.272	22.751	22.916
head width	F	4.68	15.45*	1.42		
Diam. Tymp./	Mean sq.	335.818	8.049	69.134	31.196	31.850
diam. eye	F	10.54*	0.25	2.22		
Interocular/	Mean sq.	1524.029	160.536	109.399	96.530	96.751
internasal	F	15.75*	1.66	1.13		
Internasal/	Mean sq.	....	....	24.723	1.778	....
head width	F			13.91*		
Ant. eye-nares/	Mean sq.	435.558	22.770	4.850	10.146	10.054
ant. eye-snout	F	43.32*	2.26	0.48		
Length femur/	Mean sq.	250.096	2.976	14.597	4.208	4.388
snout-anus	F	57.00*	0.68	3.47		
Tibia/	Mean sq.	....	....	47.982	6.369	....
snout-anus	F			7.53*		
Length femur/	Mean sq.	208.99	5.78	40.86	15.92	16.35
length tibia	F	12.78*	0.35	2.57		
Length tarsus/	Mean sq.	69.36	1.08	4.82	76.83	75.58
length femur	F	0.92	0.01	0.06		
Length femur/	Mean sq.	156.512	118.885	4.011	8.705	8.624
hind foot	F	18.15*	13.79*	0.46		
Length tarsus/	Mean sq.	5.48	33.38	0.005	2.91	2.86
hind foot	F	1.92	11.67*	0.001		
Fourth toe/	Mean sq.	78.762	5.631	3.220	11.461	11.310
hind foot	F	6.96*	0.50	0.28		

* Indicates significant F values.

three species is represented by forty specimens. The sexes are set up in two rows, male and female. There is one of these designs for each of the fourteen ratios.

Significant interaction in this study indicates that sexual dimorphism, if present, is not the same in all the species concerned. If interaction is not significant then sexual dimorphism, if present, has the same relationship in all the species.

The level of significance used throughout the analysis of variance is 1%. Since the degrees of freedom for the error mean square are one hundred fourteen (114), for interaction mean square two (2), for row (sex) mean square one (1), and column (species) two (2), the critical regions are as follows: interaction, F greater than 4.81; species, F greater than 4.80; and sex, F greater than 6.86.

The method of least significant difference (LSD) is used to separate the species means. The formula used is $x_1 - x_2 > t\alpha\sqrt{\frac{2s^2}{N}}$. The quantity to the right of the inequality is called the LSD between the two means x_1 and x_2. $t\alpha$ is the students t distribution value at α significance level, s^2 is the error

TABLE 2.—Means with extreme observations of each ratio for each species and sex. The middle of the three numbers is the mean, the two outer, the extremes.

Ratio		R. aurora			R. cascade			R. pretiosa		
Head width/	♂	31.86	35.93	38.24	33.98	36.36	38.92	32.83	36.19	41.09
snout-anus	♀	32.16	36.88	39.87	33.88	36.75	40.35	32.03	35.38	38.14
Head length/	♂	29.32	32.35	35.10	28.98	31.38	33.85	27.63	30.83	34.01
snout-anus	♀	29.31	31.43	33.60	28.08	30.72	35.07	27.83	29.32	31.25
Head length/	♂	78.39	90.14	100.49	78.33	86.40	94.62	76.50	85.30	94.77
head width	♀	75.62	84.66	91.91	77.72	83.66	92.08	74.07	83.21	93.90
Diam. tymp./	♂	45.71	59.17	73.44	49.25	59.35	73.59	54.39	66.37	73.77
diam. eye	♀	55.56	62.04	70.33	50.62	60.37	68.33	52.00	64.05	73.26
Interocular/	♂	63.64	74.36	83.72	54.55	75.88	102.04	73.53	86.36	107.69
internasal	♀	63.33	80.33	100.00	56.00	75.41	91.31	62.79	87.81	109.76
Internasal/	♂	20.09	22.17	23.89	19.50	22.45	24.14	15.25	16.98	19.61
head width	♀	15.26	19.54	22.54	20.53	22.96	25.00	12.96	15.95	18.29
Ant. eye-nares/	♂	41.76	44.76	48.28	35.64	46.05	53.85	44.68	51.26	56.76
ant. eye-snout	♀	41.13	45.32	51.49	41.75	47.72	52.43	41.78	51.64	58.77
Length femur/	♂	48.11	52.51	55.08	49.54	51.97	55.74	45.16	48.90	53.63
snout-anus	♀	45.47	53.11	60.00	49.05	53.32	57.96	43.88	47.89	51.99
Length tibia/	♂	47.85	55.69	59.81	51.73	55.93	59.08	48.17	50.90	54.46
snout-anus	♀	51.18	57.13	67.40	53.49	57.32	61.35	45.83	48.52	51.75
Length femur/	♂	88.08	94.58	113.74	87.38	92.99	100.34	91.11	96.06	100.99
length tibia	♀	86.56	93.17	100.22	81.66	93.12	100.00	93.13	98.66	106.02
Length tarsus/	♂	52.22	59.57	65.76	54.30	57.47	62.96	56.16	60.55	65.04
length femur	♀	52.57	59.73	63.64	52.31	57.73	69.64	56.45	59.56	62.91
Length femur/	♂	56.26	60.77	64.83	58.95	64.32	70.38	56.25	60.45	65.38
hind foot	♀	57.77	62.41	70.68	58.52	65.93	73.51	58.42	63.17	67.56
Length tarsus/	♂	31.10	36.18	40.14	35.18	36.91	38.95	32.60	36.58	39.13
hind foot	♀	32.57	37.25	40.98	32.96	37.99	40.70	33.58	37.60	40.17
Fourth toe/	♂	66.67	70.36	75.75	66.05	69.98	72.87	66.87	72.50	77.99
hind foot	♀	66.19	69.31	79.14	65.02	70.04	74.94	46.17	72.19	77.69

mean square of the analysis of variance, and N is the number of observations per sample. The 5% significance-level is used in this test. Therefore t_{α} is equal to 1.98.

Summary of statistical data.—The results of the statistical analysis are tabulated in tables 1-4. Those ratios that are significant are so indicated by the presence of an asterisk. Table 1 gives the F values for species, sex, and interaction. If species is significant as shown in Table 1 then refer to Table 3 in order to ascertain where the species difference lies. If sex is significant then refer directly to Table 2 which shows the means of the ratios for each species and sex. If interaction is significant then the analysis of variance is broken down and species and sex are analyzed sperately as in Table 4.

The following comparisons of the species and sex are based on the statistical significance or lack of significance of the mean ratios used in this study. The conclusions are valid for these data and the levels of significance used. Comparisons are, unless otherwise stated, relative to body length.

SEX

The head is relatively shorter in the females than in the males of all three species, whereas the head widths are equal relative to body length, in all three species.

The internasal distance is wider, relative to head width, in the males of

TABLE 3.—Those ratios significant for species and interaction showing least significant differences (LSD) as compared with the actual differences (M_2-M_1), (M_3-M_2) between the species means.

Ratio	LSD α.05	(R.——) M_1	M_2-M_1	(R.——) M_2	M_3-M_2	(R.——) M_3
Head length/ snout-anus	0.691	R. pretiosa 30.109	0.943*	R. cascadae 31.051	0.841*	R. aurora 31.892
Diam. tymp./ diam. eye	2.499	R. cascadae 59.862	0.742	R. aurora 60.604	4.606*	R. pretiosa 65.210
Interocular/ internasal	4.355	R. cascadae 75.644	1.702	R. aurora 77.346	9.739*	R. pretiosa 87.085
Internasal/ head width	♂—0.729 ♀—0.936	R. pretiosa 16.982 15.951	5.185* 3.587*	R. aurora 22.167 19.538	0.278 3.422*	R. cascadae 22.445 22.960
Ant. eye-nares/ ant. eye-snout	1.404	R. aurora 45.040	1.842*	R. cascadae 46.882	4.567*	R. pretiosa 51.449
Length femur/ snout-anus	0.927	R. pretiosa 48.397	4.249*	R. cascadae 52.646	0.160	R. aurora 52.806
Length tibia/ snout-anus	♂—1.503 ♀—1.684	R. pretiosa 50.898 48.520	4.794* 8.609*	R. aurora 55.692 57.129	0.234 0.191	R. cascadae 55.926 57.320
Length femur/ length tibia	1.790	R. cascadae 93.055	0.823	R. aurora 93.878	3.483*	R. pretiosa 97.361
Length femur/ hind foot	1.300	R. aurora 61.593	0.214	R. pretiosa 61.807	3.314*	R. cascadae 65.121
Fourth toe/ hind foot	1.490	R. aurora 69.832	0.179	R. cascadae 70.011	2.336*	R. pretiosa 72.347

* Indicates significant differences.

R. aurora than in the females. This is true, however, only in *R. aurora* for there is no significant dimorphism in the sexes of the other two species.

In none of the species was there significant sexual dimorphism in femur length. However, the tibia of the females of *R. pretiosa* is shorter relative to snout-anus length, than in the males.

The hind feet of females in all the species are shorter relative to the femora and consequently to body length, than those of the males. Furthermore, on the basis of these mean ratios the tarsus comprises more of the foot in females than in males.

SPECIES

The head width in all three species is relatively the same. Relative head length, however, differs between all three species. Thus, the head of *R. pretiosa* is the shortest of any of the species, and that of *R. aurora* the longest. The head of *R. cascadae* is intermediate between the two. Relative to head width, the internasal space differs between all three species. The internasal distance is the widest in *R. cascadae*, narrowest in *R. pretiosa* and intermediate in *R. aurora*. If only males are considered the width is not different between *R. aurora* and *R. cascadae*.

The interocular space is wider in *R. pretiosa*, relative to the internasal space, than that of the other two species. The latter do not differ between themselves. Since, as mentioned above, the internasal width is narrower in *R.*

TABLE 4.—Those ratios in which interaction is significant and in which the sex and species are treated separately.

Ratio		Variation due to	D.f.	Mean square	F	Critical region
		A. SEX				
		Sex	1	69.127	33.76*	F>7.36
	R. aurora	Error	38	2.048		
Internasal/		Sex	1	2.656	1.51	F>7.36
head width	R. cascadae	Error	38	1.702		
		Sex	1	10.642	6.71	F>7.36
	R. pretiosa	Error	38	1.585		
		Sex	1	20.654	1.70	F>7.36
	R. aurora	Error	38	12.151		
Length tibia/		Sex	1	19.431	4.21	F>7.36
snout-anus	R. cascadae	Error	38	4.617		
		Sex	1	56.563	24.17*	F>7.36
	R. pretiosa	Error	38	2.340		
		B. SPECIES				
		Species	2	189.308	142.39*	F>5.01
Internasal/	Male	Error	57	1.329		
head width		Species	2	245.693	112.09*	F>5.01
	Female	Error	57	2.192		
		Species	2	161.026	28.51*	F>5.01
Length tibia/	Male	Error	57	5.648		
snout-anus		Species	2	505.284	71.27*	F>5.01
	Female	Error	57	7.090		

* Indicates significant F values.

pretiosa there may be little or no actual difference between the relative width of the interocular spaces of the three species.

The diameter of the eye relative to the tympanum is smaller in *R. pretiosa* than in the other two species.

Relative to snout length the nares are nearest the tip of the snout in *R. pretiosa* and furtherest from the tip in *R. aurora,* while those of *R. cascadae* are intermediate in position.

Both the tibia and the femur are shorter in *R. pretiosa* than in the other two species. *R. cascadae* and *R. aurora* are not significantly different in these characters. Similarly, in relation to the femur, the tibia of *R. pretiosa* is shorter than that of either *R. cascadae* or *R. aurora.* Therefore, the shorter legs of *R. pretiosa* are due not to an equally proportional reduction of both leg segments, but rather to a somewhat more drastic reduction of the tibia than of the femur.

Relative to the femur, the tarsi of all three forms are the same. Therefore in accordance with the greater reduction of the tibia in *R. pretiosa,* the tarsus is somewhat longer in proportion to the entire leg. The hind foot, relative to the femur, is smaller in *R. cascadae* than in the other two forms. This would indicate that in relation to leg length the feet of *R. cascadae* are smaller than the feet of the other two forms. However, in relation to body length it is smaller only in comparison to *R. aurora,* and is nearly equal to that of *R. pretiosa.* The fourth toe of *R. pretiosa* comprises a greater portion of the foot than in either of the other two species.

The number of characters the three forms have in common is indicated below. Ra refers to *R. aurora,* Rc to *R. cascadae,* and Rp to *R. pretiosa.* A dash between the symbols signifies that they differ; if no dash is present, then there is no difference. Thus, the three forms differ from each other with regard to three characters (Ra—Rc—Rp. . . 3). In no instance in the ratios were *R. cascadae* and *R. pretiosa* the same but differed from *R. aurora* (Ra—Rc Rp. . . 0). In seven cases *R. aurora* and *R. cascadae* ratios were the same but differed from *R. pretiosa* (RA Rc—Rp...7). In one case *R. aurora* and *R. pretiosa* were the same but differed from *R. cascadae* (Rc—Ra Rp . . . 1) and in four cases of the fifteen all three forms were similar (Ra Rc Rp . . . 4).

If we conclude that frogs with the most characters in common are the more nearly related, then *R. cascadae* and *R. aurora* would be closer than *R. cascadae* and *R. pretiosa,* or *R. aurora* and *R. pretiosa.* Relationships based on similarities must be given careful consideration in order to exclude the possibility of convergent or parallel evolution among possibly rather remotely related forms.

This analysis also indicates that a considerable amount of sexual dimorphism is present in frog populations. The dimorphism may be small and hardly discernible in samples of very few individuals, but with these data it is evident. The tendency for sexual dimorphism in a character, when present, to occur in all three forms is evident. However the deviation from this tendency in two ratios is interesting (Internasal/head width in which sexual dimorphism is present in *R. aurora,* but not in the other two, and the tibia/snout-anus length in which it is present in *R. pretiosa* but absent in the others).

Most of these ratios are practically useless in assigning individuals to species, since the overlap is great. However, they are useful in defining populations of organisms, the study of which is heavily emphasized in modern

systematics. It must be pointed out however, that statistical significance may or may not have taxonomic significance, for statistical significance merely implies that a difference exists. The difference may be the result of either environmental or hereditary characteristics, but statistics as such does not distinguish between these differences. Furthermore, statistical significance may be found between local populations within a subspecies, between subspecies of a species, or between species of a genus. It is up to the worker to correctly define the populations with which he is working, to have some idea of the variation to be encountered in the population, and so to evaluate the statistical significance or lack of significance encountered.

Ventral color.—The bright colors of the ventral surfaces of living frogs were examined to determine the amount of variation present. These colors were found to be quite consistent.

All adult *R. aurora* examined had red on the ventral surface, although there was considerable individual variation in intensity and extent. The color ranged from bright red on the ventral surfaces of the hind legs, along the sides of the body and undersurfaces of the forelegs, and in scattered flecks on the abdomen, to a very pale red on the ventral surfaces of the hind legs only.

All adult specimens of *R. cascadae* were various shades of yellow or buff on the ventral surfaces of the body.

The adult specimens of *R. pretiosa* from the Willamette Valley, and the eastern flank of the Cascades were bright reddish-orange on the ventral surface of both pairs of limbs, along the sides, and in a few scattered patches on the abdomen. *R. pretiosa* from Mill Creek and the John Day River area were more of an orange or yellow-orange below. The latter follow the ventral color of *R. p. luteiventris* as described by Thompson (1913) more closely than do those from the eastern flank of the Cascades.

In no instance were specimens collected that showed overlap or intergradation on the basis of these bright ventral colors.

Groin.—Wright and Wright (1949) state that Slater compares the three frogs on the basis of coloration and extent of mottling in the groin. The groin of *R. pretiosa* is red and not mottled; that of *R. cascadae* is mottled somewhat, with the lower sides yellowish-cream; *R. aurora* is always heavily mottled with black and is colored red, yellow and green.

All of the living adult *R. pretiosa* noted in this study had red in the groin, but a few (10%) had very faint gray mottling present in the groin. It is of interest that this mottling was most pronounced in specimens from northeastern Oregon.

FIG. 2.—Degree of groin mottling in the three species. Left to right: *R. aurora*, *R. cascadae*, and *R. pretiosa*.

The living *R. aurora* all had some yellow in the groin, some had red, and a few had a hint of green. The black mottling, however, was very prominent and only about 2% of them could be confused with the next most mottled form, *R. cascadae*. Living *R. cascadae* from the area studied, all had bright yellow or yellow-green in the groin region. *R. cascadae* was typically less distinctly mottled than *R. aurora* but more so than *R. pretiosa* (fig. 2).

Thus, it may be seen that in preserved specimens in which the color has disappeared, but the mottling has remained, the majority of the specimens may be definitely placed in one species or another on this one character alone. In living specimens where both groin mottling and color may be taken into consideration, all specimens examined could be placed into the proper species.

Dorsal spotting.—Each species of frog has one or more kinds of dorsal spotting which is quite typical for that species. There may be some overlapping between forms, but the majority of individuals with a certain type of spotting may be assigned to the correct species on the basis of spotting alone.

R. aurora has two general types of spotting that are rather typical. One consists of more or less indistinct, irregular black spots, usually two or three millimeters in diameter, with many tiny black flecks between them (fig. 3). The other consists of a reticulum of black line over all the dorsum.

FIG. 3.—Dorsal views of adult female frogs showing spotting "typical" of the three species. Left to right: *R. aurora*, *R. cascadae*, and *R. pretiosa*.

The spotting of *R. cascadae*, although quite variable always consists of black spots of various shapes, invariably with very distinct margins. (fig. 3). Very seldom is there a peppering of tiny flecks between these larger spots, as in the case in *R. aurora*.

In *R. pretiosa* the spotting typically consists of large, usually rather indistinct spots, generally with light centers (fig. 3). The light centers are sometimes also found in the spotting of *R. cascadae* but seldom do the light centered spots form the majority in any one specimen of this form.

Examination of the spotting of a group of specimens revealed that of eighty-eight *R. cascadae*, eighty-six (97.72%) were typical, one (1.14%) similar to *R. aurora*, and one (1.14%) resembled *R. pretiosa;* of sixty-six

R. aurora, sixty (90.91%) were typical and six (9.09%) were similar to *R. cascadae;* of sixty-nine *R. pretiosa*, sixty-six (95.65%) were typical and three (4.34%) were similar to *R. cascadae*. The greatest overlap seems to be between *R. aurora* and *R. cascadae* with 7 of 154 individuals overlapping. It may be seen that while the type of spotting may be an aid in allocating a specimen to its species, it is not by itself an infallible character.

Metatarsal tubercles.—The number of metatarsal tubercles is one of the characters often used in distinguishing between the two subspecies *R. p. pretiosa* and *R. p. luteiventris*. In the material examined every stage in the transition between one and two tubercles was found, so it often was a matter of personal judgment as to whether one or two were to be recorded. I have therefore reviewed this character critically.

Of sixty-six *R. aurora* examined, forty-five (68%) had two metatarsal tubercles on each hind foot and twenty-one (32%) had only one tubercle evident. Most of the literature describes *R. aurora* as having two tubercles. The number of tubercles present on any one individual seemed scattered indiscriminately throughout the collecting area, and both one and two were found in both sexes.

R. cascadae, likewise is described (Slater, 1939) as having two metatarsal tubercles. However, on examination, eleven (13%) of eighty-three individuals had only one while the remaining seventy-two (87%) had two metatarsal tubercles. Again both counts were found throughout the area studied.

R. pretiosa luteiventris reportedly has one metatarsal tubercle as opposed to two in *R. p. pretiosa* (Thompson, 1913). Wright and Wright (1949) following Gordon (1939), tend to consider the *R. pretiosa* in western Oregon *R. p. pretiosa* and those east of the Cascade crest as *R. p. luteiventris*. Of seven adult *R. pretiosa* collected in the Willamette Valley in western Oregon, four had two tubercles and three had one. Of sixty-four collected east of the Cascade crest, sixty (94%) had one tubercle and four (6%) had two. If the number of metatarsal tubercles is considered a reliable subspecific character, then on the basis of this small sample, the Willamette Valley population is an intergrade in this character between the two subspecies. The eastern Oregon group, however, tends more toward *R. p. luteiventris*.

Relative length of leg.—The length of the hindleg, in relation to the head and body length has often been used to distinguish between *R. pretiosa* and the other two forms (Stebbins, 1951; Wright and Wright, 1949). This is done by extending the leg along the side or back of the frog and noting where the flexed tibio-tarsal joint reaches. In *R. pretiosa* the heel usually does not reach the external nares while in *R. aurora* and *R. cascadae*, it usually reaches to or beyond this point. The use of preserved specimens made this character rather difficult to determine, but comparison on animals before and after preservation indicated that the method is valid if a uniform technique is used. The heels of sixty-six *R. aurora* were measured and four (7.57%) were short of, three (4.55%) reached, and fifty-nine (87.88%) extended beyond the nares. In similar measurements of the heels of ninety-five *R. cascadae* nine (9.49%) did not reach, six (6.33%) reached, and eighty (84.24%) extended beyond the nares. Of seventy-five *R. pretiosa* examined,

the heels of only three reached, while the remainder, seventy-four (96.10%), were short of the nares.

This indicates that, at least with preserved specimens, the leg to the heel is not always proportionally shorter in *R. pretiosa* than in the other two. Of the seven *R. aurora* with heels to or short of the nares, five were from areas above 2100 feet elevation; while only two were below this altitude. Indeed, only seven were collected above 2100 ft., so 71% of those above 2100 ft. had relatively short legs. This tendency in *R. aurora* for shorter legs might be environmental in view of Schmidt's work on leg length in relation to latitude (1938). However, the small size of the sample prevents any definite conclusions.

The fifteen short legged *R. cascadae* come from all parts of the range with no apparent correlation to altitude. In most collecting areas only one or two short legged individuals would be found in a series. In Salt Creek, however, four of five specimens were short legged. This is rather interesting in view of the fact that four of five *R. aurora* from the same area were short legged.

Thus, we must conclude that while the relative length of the leg is a helpful taxonomic character and holds in the majority of the cases, it is by no means infallible and must be used in conjunction with other characters.

Skin texture.—In this study, three general groups of skin texture were set up. The first, designated group 1, varied from completely smooth individuals to those having a very fine granulation in the tibial and tarsal regions, and resulting in frogs with a few low tubercles on the back and sides. Group 2 varied from very fine granulation over legs, back and sides to those with this granularity plus tubercles on the sides and back. The smoothest individuals in group three had fine granulation all over the dorsal surface (excluding part of the head) plus many closely crowded large pointed tubercles on the legs and sides. The extremely rough individuals of the latter group had large tubercles crowded all over the dorsal surface in addition to the legs and sides. Of sixty-seven *R. aurora* examined sixty (89.55%) belonged to group 1 and seven (10.45%) were in group 2. Fifteen (14.85%) of one hundred and one *R. cascadae* were in group 1, eighty-four (83.17%) in group 2, and two (1.98%) in group 3. Two (2.67%) of seventy-five *R. pretiosa* belonged to group 2 and the remainder, seventy-three (97.33%), were in group 3. From this it may be seen that *R. cascadae* overlaps both other species.

The skin texture of this form in the Cascade Mountains of Oregon is quite remarkable since it varies from completely smooth to very rough. Furthermore, individuals of *R. cascadae* from one locality may show practically the same range of variation in this character as a collection of *R. cascadae* from all over the area studied. The seven *R. aurora* that fall within group 2 most resemble the smoothest specimens of that group, while the *R. pretiosa* resemble the roughest. Thus, no specimens were found in which *R. aurora* and *R. pretiosa* overlap on this character. The texture of the skin serves to separate *R. aurora* and *R. pretiosa* but not *R. cascadae* from either other form.

Distribution of ventral melanophores.—Melanophores were found to be present over the entire ventral surface of *R. aurora* and *R. pretiosa* although often microscopic examination was necessary before they could be seen. *R. cascadae* in contrast to the other two forms, normally has a large melanophore free area in the median abdominal region. Specimens were examined to see

if this character held good over a series. Fifty-nine (98.33%) of sixty *R. aurora* possessed melanophores on the ventral surface and in only one (1.67%) were they lacking on abdomen. Ninety-seven (98.98%) of ninety-eight *R. cascadae* exhibited no ventral melanophores and with but one (1.02%) exhibiting these structures. Seventy-one (95.95% of seventy-four *R. pretiosa* possessed ventral melanophores and three (4.05%) were free of them.

This character serves very well as an aid in distinguishing *R. cascadae*. Practically all of the *R. aurora* were heavily covered with melanophores below. In a few specimens, they became rather dilute, and in one specimen were practically absent from the median abdominal area. The *R. pretiosa* examined from western Oregon, and the east slope of the Cascades were all heavily covered with melanophores below. In eastern Oregon, however, along with the reduction in color, there occurs a scattering of these ventral melanophores. The three melanophore free *R. pretiosa* represent the completion of this trend in a few individuals. As is true in several other characters, the *R. pretiosa* from eastern Oregon in which the abdominal melanophores tend to thin out, are separated from *R. cascadae* which lack these melanophores by a strip of *R. pretiosa* along the east slope of the Cascades in which heavily mottled abdomens are the rule.

Habitat Preference

Non-breeding adult *R. aurora* were usually found among down logs, in blackberry tangles or other types of dense cover. Upon being disturbed they would immediately make an attempt to escape into the nearest pool or stream. The greatest departure from this habitat type was in some deep, steep banked, man-made pools on Coffin Butte (Benton County). These pools are permanent and have only a few clumps of young willows along the edges. Furthermore, there is little other cover available for a great distance. In this area the frogs sit on the banks of the pools very close to the edge of the water, and if disturbed dive into the water. Often they would not attempt to hide in the vegetation on the bottom of the pool, but merely crouch on the bottom in plain view through the clear water of these ponds.

Specimens of *R. pretiosa*, on the other hand, were usually first seen floating in the water among sedges (*Carex*) and pond weed (*Potamogeton*). Specimens were found most abundantly in pools and lakes which had a well developed stand of sedge, pond weed or water lily in rather shallow water. The six inches to a foot and one half of loose muck that covers the bottom of such areas is an excellent hiding place. The frogs can dive into the muck, swim through it a short distance and hide. *R. pretiosa* was also found on the bank in the edge of the water along small pools and ditches. It was never found as far away from the water as was *R. aurora*.

Non-breeding individuals of *R. cascadae* were found most abundantly along small mountain streams where they sat on the bank in the grass and shrubs. When disturbed they would dive into the stream, but instead of trying to hide on the bottom would either swim across the stream if very narrow, or would swim down the stream for a few feet and climb partially out on the bank. The frogs would even hesitate to dive into some of the swifter, colder streams. In some areas *R. cascadae* was found in rather shallow, warm ponds. In these pools the behavior was considerably different. Upon diving into one

of these pools the frog would immediately submerge and swim along the bottom until it found something to hide under. This is much more similar to the behavior observed in *R. aurora* and *R. pretiosa*.

From the foreging observations it would appear that *R. pretiosa* is the most highly aquatic form of the three, while *R. aurora* tends to spend much more time on land. *R. cascadae* appears to be less aquatic than *R. pretiosa* but was not often observed as far from the water as *R. aurora*.

DISCUSSION AND CONCLUSIONS

The results of the statistical analysis based on various ratios on three groups of frogs which were diagnosed as belonging to *R. aurora*, *R. cascadae*, or *R. pretiosa*, indicate that *R. cascadae* is most closely allied to *R. aurora*.

No intergrading or overlapping was observed in ventral coloration between *R. cascadae* and the other two forms, since *R. aurora* and *R. pretiosa* are always reddish below and *R. cascadae* is yellowish or buff. The ventral coloration of *R. pretiosa* from eastern Oregon tends to fade out and approach that of *R. cascadae*, but is more orange than that of *R. cascadae*. Furthermore, *R. cascadae* is geographically separated from the light ventered *R. pretiosa* by a strip containing *R. pretiosa* with bright red ventral surfaces.

In adult living animals, three groups representing *R. aurora*, *R. cascadae*, and *R. pretiosa* may be distinguished on the basis of groin markings and color. These groups do not overlap since *R. aurora* is yellow and red with heavy black mottling, *R. cascadae* is yellowish-green with some dark mottling, and *R. pretiosa* is red, usually without mottling. Specimens that have been preserved for some time, however, lose the bright groin colors, but usually retain the dark mottling. The majority, but not all preserved specimens examined from Oregon could be placed in the correct group on the distinctness of mottling alone.

The dorsal spotting of each of the three groups is quite distinctive. In none of the specimens examined did *R. aurora* have the large indistinct spots of *R. pretiosa*, nor did *R. pretiosa* have the many small black flecks characteristic of so many *R. aurora*. Several *R. aurora* (9%) had the large, distinct, black spots of *R. cascadae*, but only one *R. cascadae* even approached the *R. aurora* type of spotting. The overlap in this character between *R. cascadae* and *R. pretiosa* was present but very small.

The metatarsal tubercles, at least in the Oregon frogs, are not as fixed in number as the literature would lead one to believe. *R. aurora* and *R. cascadae* reportedly have two metatarsal tubercles on each hind foot, but only 68% of the *R. aurora* examined in this study had two and 32% had one, while 87% of the *R. cascadae* had two and 13% had one. *R. pretiosa pretiosa* is reported to have two metatarsal tubercles while *R. p. luteiventris* is characterized by one. The *R. pretiosa* of western Oregon are usually considered to be *R. pretiosa pretiosa* and those east of the Cascades *R. p. luteiventris*. Of seven examined from western Oregon, four had two and three had one, while of sixty-four from east of the Cascade crest, 94% had one tubercle and 6% had two.

R. aurora and *R. cascadae* reportedly, may be separated from *R. pretiosa* on the basis of relative leg length, the heel of the extended hindleg reaching beyond the nostrils in the former two, and the heel short of the nostrils in

the latter one. Of sixty-six *R. aurora* examined for this character, in 12% the heel reached to or short of the nostrils and in 88% it reached beyond. In *R. cascadae* the heel of 16% of the ninety-five animals examined reached to or short of the nares and that of 84% beyond. The trend was reversed in *R. pretiosa* in which 4% of the seventy-seven examined reached the nares and the other 96% were short of the nares.

The skin of *R. aurora* is generally quite smooth and in no specimen examined did it even approach the roughness characteristic of *R. pretiosa*. *R. cascadae* however, is extremely variable in this character, with individuals from the same locality showing every degree of roughness encountered in this study.

The distribution of the ventral melanophores is a character that tended to separate the majority of *R. cascadae* from the other two forms. The melanophores were usually found to be absent from the medial abdominal area of *R. cascadae* but present in the other two forms.

As a habitat *R. aurora* seems to prefer cool densely covered land areas in the vicinity of slow streams or near ponds or sloughs in the lower elevations of western Oregon. *R. pretiosa*, on the other hand, seems to be much more aquatic since it spends much of its time in the water and seldom ventures far from the edge of the pool. This species is wide ranging in eastern and western Oregon and seems to be absent only from the northern Oregon Cascades. *R. cascadae* is a mountain form dwelling along small mountain streams, ponds or lakes. It seems to prefer the edges of the banks of the streams or lakes, very seldom spending much time floating in the water after the manner of *R. pretiosa*.

On the basis of this study I am inclined to believe that the three groups studied are species. *R. aurora* and *R. pretiosa* are very distinct from one another, being distinguished by the color and amount of groin mottling, the relative length of the hindlegs, dorsal spotting, roughness of the skin, the general body proportions as shown in the statistical section, and habits. A further item, not mentioned before in this study is the tendency for the eyes of *R. pretiosa* to be oriented more dorsally while those of *R. aurora* are more lateral (Stebbins, 1951). Furthermore, the eyes of *R. pretiosa* are brighter yellow while those of *R. aurora* tend to be more orange or bronze. These two eye characters taken together lend the head of *R. pretiosa* a strikingly different appearance from that of *R. aurora*. The fact that both of these forms are found in western Oregon in the same ponds should dispel doubts of their specific distinctness.

While *R. cascadae* has been more of a problem, examination of living specimens leaves no doubt the *R. cascadae* is distinct from the other two, whether specifically or subspecifically so. The most obvious point of difference of *R. cascadae* from *R. aurora* and *R. pretiosa* is the yellow or buff ventral coloration and the yellowish green, slightly mottled groin of *R. cascadae*. As mentioned above, the author found no signs of intergradation in these, although in distribution *R. cascadae* overlaps *R. aurora* on the west and *R. pretiosa* on the east. If genetic interchange were taking place, it would seem that intermediates would be present, unless of course, the color pattern is dependent on a single factor. *R. cascadae* differs further from the other two species by the lack of median abdominal melanophores, the rather distinctive type of spots, and in the habitat preference. It may be distinguished from

R. pretiosa by the longer legs, reduced webbing on the hindfeet, and the generally greater smoothness of the skin. Additional points of difference from *R. aurora* are the yellow, almost *R. pretiosa* like eyes, and the greater roughness of the skin in most specimens. Although it more resembles *R. aurora* in general body proportions than it does *R. pretiosa*, *R. cascadae* is rather intermediate between the other two forms in other characters such as skin textures and groin mottling.

Although specimens of *R. pretiosa* examined from western Oregon and parts of eastern Oregon were in rather small series, there would seem to be ample reason to separate the Oregon representatives of the species into the two subspecies, *R. p. pretiosa* in western Oregon and *R. p. luteiventris* in Oregon east of the Cascades. The frogs of the two areas differ in ventral coloration, those in eastern Oregon being orange-red; in the distribution of the abdominal melanophores, those from the eastern part of Oregon being more widely dispersed; and in the proportion of animals having two metatarsal tubercles to those having one. The greater number of *R. pretiosa* from eastern Oregon have one and those from western Oregon have two metatarsal tubercles. The series from the eastern slope of the central Oregon Cascades, are interesting in that they closely resemble western Oregon forms in all the above mentioned characters except the metatarsal tubercles. In the latter character they follow the rest of the eastern Oregon *R. pretiosa* and thus might be considered intergrades between the two subspecies.

SUMMARY

A study, of the distribution and relationships of *R. aurora*, *R. cascadae* and *R. pretiosa* in Oregon is undertaken. A majority of the specimens examined were collected from an area in west-central Oregon with dimensions of approximately one hundred and forty miles by eighty miles.

The taxonomic status of the frogs has been briefly summarized.

R. pretiosa is distinguished from the other two forms by the shorter legs, greater amount of webbing, lack of mottling on the sides, lack of a mask and the greater roughness of the skin. *R. aurora* is distinguished from *R cascadae* by the red ventral color of *R. aurora* as opposed to the yellowish venter of *R. cascadae*, by the red, and yellow heavily mottled groin of *R. aurora* compared with the yellowish lightly mottled groin of *R. cascadae*, by the greater roughness of the skin in *R. cascadae*.

Three species are recognized, *Rana aurora*, *R. cascadae* and *R. pretiosa*, the latter with two subspecies of *R. p. pretiosa* and *R. p. luteiventris*. *R. aurora* and *R. pretiosa* are the most distinct of the forms while *R. cascadae* most closely resembles *R. aurora* in its external morphology, but in some characters is intermediate between *R. aurora* and *R. pretiosa*.

The distribution of the frogs in Oregon may be summarized as follows: *R. aurora* occurs in western Oregon east into the lower foothills of the western slope of the Cascades. *R. pretiosa* occurs all over the state, except the higher parts of the northern Oregon Cascades, in two subspecies, *R. p. pretiosa* west of the Cascades and *R. p. luteiventris* in eastern Oregon. *R. cascadae* is found in a narrow strip down the Cascades at least as far south as Crater Lake.

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Food Habits of the Bullfrog in Central Missouri Farm Ponds[1]

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The bullfrog (*Rana catesbeiana* Shaw) is an important, widely distributed game species, but its food habits have not been thoroughly investigated. This paper reports a study of the food habits of bullfrogs in central Missouri. Data were derived from the examination of 455 stomachs of bullfrogs secured from farm ponds between the inclusive dates, April 11, 1950, to October 21, 1951. Eighty-seven stomach samples were collected during 1950 and 368 during 1951. Specimens were obtained for almost the entire time that bullfrogs were out of hibernation over a two-year period, which permitted a study of seasonal changes in feeding habits.

Review of Literature

Most references dealing with food habits of the bullfrog are general in context, or result from an inconclusively small number of samples. Several reports are mere notes of interest concerning the feeding of a single frog.

Among the early authors, Needham (1905), who worked in New York, concluded from examination of 16 bullfrog stomachs that the most important foods were insects and snails. A total of 164 prey animals were identified. In addition to insects, he found 18 snails, 3 crustaceans, 3 spiders, and 2 vertebrates.

Dyche (1914) examined stomachs of 30 bullfrogs taken from fish hatchery ponds in Kansas. He found that 14 of the 30 samples contained 32 fish. Otherwise, the diet was made up largely of crayfish, insects, spiders, and snails.

Frost (1935) summarized the findings of several early authors, as follows:

"Although Dickerson (1907) remarks that bullfrogs are known to eat young water birds . . . birds are a somewhat rare diet in nature. Surface (1913) summarizes the food, determined by the dissection of 39 bullfrogs, as follows: 29 contained food which included earthworms, crayfish, spiders, insects, and a young frog. Holbrook (1842) states that insects and small animals, such as crayfish and snails, constitute the food of the bullfrog. Wright (1920) says that small fish, young ducklings, sparrows, snakes, and a young alligator have beeen taken from bullfrog stomachs. Palmer (1908) is one

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of the few who found a mouse in the stomach of a bullfrog. Dickerson (1907) adds the turtle to the list of food of *Rana catesbeiana*."

In his own work, Frost (1924) included the bullfrog with five other species when he reported on frogs as insect collectors. He found that insects formed the principal foods of these species, but a possible exception was the bullfrog, which was "more often filled with Crustacea and Arachnida." Later, Frost (1935) stated that insects formed the chief food of smaller bullfrogs, but that spiders and snails formed the greatest proportion of food of the larger ones. The later statement was based on examination of 25 stomachs.

Another study which involved the analysis of a specified series of bullfrog stomachs was made by Perez (1951) in Puerto Rico. This study was made to learn whether bullfrogs were injurious to pollywogs or small adult toads which had been imported for cane-borer control. He examined 50 stomachs, and found that insects and other small animals were taken in nearly equal proportions. He added that practically none of the food items was beneficial to man.

The importance of crayfish in the diet of bullfrogs was shown by Baker (1942) and Penn (1950). Baker stated that in eastern Texas crayfish were the principal food of bullfrogs. Penn reported upon the utilization of crayfish by cold-blooded vertebrates and showed, from data secured by Needham (1905) and Frost (1935), that crayfish comprised approximately 26 percent of the bullfrog diet.

Several writers have recorded the taking of seemingly unusual prey items by individual bullfrogs. These include ducklings (McAtee, 1921); a 17-inch coral snake (Minton, 1949); remains of a full-grown field mouse and two downy black ducks in a single stomach (Hewitt, 1950); and two occurrences of terrestrial birds (Howard, 1950).

A general description of bullfrog food habits was provided by Dickerson (1931). She named insects, fish, small turtles, young water-birds, and frogs, as bullfrog prey. A more complete, yet general, listing of bullfrog foods was presented by Stebbins (1951).

Munz (1920) analyzed and reported upon the contents of the alimentary canals of 104 bullfrog tadpoles in process of transformation.

These studies serve to illustrate the wide variety in bullfrog foods, with many species of vertebrates, frogs included, being taken at least occasionally. However, the studies based on systematic examination of series of stomachs emphasize the importance of invertebrate foods, particularly insects, crayfish, spiders, and snails. Little attention has been given the matter of seasonal use of these foods.

PROCEDURE

The majority of specimens used in this study were collected during the hours of darkness, from late evening until midnight. Hand-grabbing, gigging, and shooting with a .22 caliber rifle loaded with shot-shell were tried as methods of capture. In each instance a strong light was used to blind the frogs. All methods proved effective, although the rifle required least time and effort.

Stomachs used in this investigation were removed from the animals soon after collection and placed in a 10% formalin solution. They later were removed from the formalin, washed, and preserved in alcohol until examined.

In analysis, the stomach was opened, the contents emptied into a 32-mesh-

per-inch sieve, and washed under the tap. The contents then were placed on blotting paper to remove excess moisture. The semi-dry food items were separated according to kind and identified, and the volume of each food was ascertained. Measurements were made in calibrated glass cylinders, and recorded as cubic-centimeters of food. Only stomachs which contained a measurable quantity of food were included. Of the stomachs examined, 20 were empty. These are not included in the total.

RESULTS

The results of this investigation are shown in graphic and tabular form in fig. 1 and tables 1 and 2, respectively. Fig. 1 depicts graphically the principal foods, by months. The percentages are based upon the monthly utilization of major foods expressed as per cent by volume, and are indicated by the vertical width of each band. Total height of the chart equals 100 per cent.

The 18 most important food groups are evaluated as to per cent by volume that each comprised of the total diet (table 1). The principal food items are listed by monthly ultilization and as percentages of the total volume of food for the two-year period.

A complete listing of all foods and miscellaneous items found in the stomach contents comprises table 2. Items are shown with percentages by occurrence and by volume, in order of importance by volume. Occurrence-percentages were obtained by dividing the total number of stomachs in which a specific item occurred by the total number of stomachs examined. Volume percentages were obtained by dividing the total volume of a specific item by the total content of all samples.

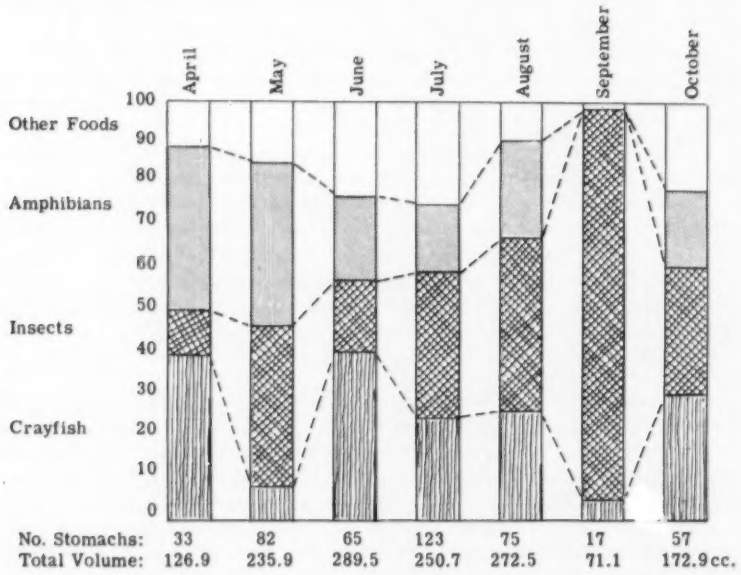

Fig. 1.—Principal Foods of Bullfrogs in Missouri, by Month.

TABLE 1.—Principal foods of 455 bullfrogs in Missouri, by month, 1950-51.
(Figures are percentages by volume. Foods which comprised less than 1.0 per cent omitted.)

Number of stomachs examined: / Month of collection:	3 March	33 April	82 May	65 June	123 July	75 Aug.	17 Sept.	57 Oct.	455 % of total food vol.
GASTROPODS									
Snails (*Physa, Planorbis, Polygyra*)	0.2	0.2	3.8	4.2	2.8	0.8	....	tr.	2.1
CRUSTACEANS									
Crayfish (*Cambarus* sp.)	31.4	39.5	7.8	40.3	24.7	26.0	4.9	30.1	26.4
INSECTS									
Water-Scavenger Beetles (Hydrophilidae)	....	8.5	8.0	0.4	7.3	25.5	12.9	2.7	9.2
Short-horned Grasshoppers (Acrididae)	....	....	....	....	0.8	2.5	67.2	17.1	6.0
Dragon-Flies and Damsel-Flies (Odonata)	....	0.5	20.4	2.0	7.0	2.4	....	....	5.5
Ground-Beetles (Carabidae)	....	0.2	2.8	8.0	2.0	3.1	2.7	3.3	3.5
Caterpillars and Moths (Lepidoptera)	....	0.2	1.4	1.5	9.2	2.3	5.2	2.9	3.3
May- and Dung-Beetles (Scarabaeidae)	....	tr.	1.7	3.8	2.2	2.1	0.3	0.1	1.9
Diving-Beetles (Dytiscidae)	0.8	tr.	1.2	tr.	1.5	0.9	4.9	1.3	1.1
Water-Bugs (Belostomatidae)	....	0.4	2.0	0.3	1.4	1.3	....	0.4	1.0
ARACHNIDS									
Spiders (Arachnida)	....	0.1	0.4	1.5	2.1	1.0	0.6	1.7	1.2
FISH									
Fish (bluegill, black bass, minnows)	....	4.9	1.7	9.3	....	1.2	....	....	2.8
AMPHIBIANS									
Frogs, Unclassified	62.8	7.1	9.8	10.1	7.8	15.6	....	16.1	11.1
Tadpoles, Unclassified	4.7	10.0	26.7	9.7	7.6	8.0	....	2.5	10.4
Toad, Unclassified	....	22.1	....	....	....	....	....	....	2.0
OTHER VERTEBRATES									
Snapping Turtle (*Chelydra serpentina*)	....	....	6.0	....	....	....	....	....	1.0
Birds, Unclassified	....	tr.	tr.	....	12.4	....	....	....	2.2
Meadow Mouse (*Microtus ochrogaster*)	....	tr.	....	4.5	3.4	....	....	12.1	3.0
PLANT MATERIALS	0.1	4.4	2.2	2.6	3.2	4.6	0.5	4.0	3.0
TOTAL	100.0	98.1	95.9	98.2	95.4	97.3	99.2	94.3	96.7
Total Volume of Food (cubic-centimeters)	12.7	126.9	235.9	289.5	250.7	272.5	71.1	172.9	1432.2

TABLE 2.—TOTAL FOODS OF 455 BULLFROGS IN MISSOURI, 1950-51

Food Item	Per Cent by Occurrence	Per Cent by Volume
ANIMAL FOODS		
Crayfish (*Cambarus* sp.)	23.5	26.4
Frogs, Unclassified	8.1	11.1
Tadpoles, Unclassified	13.4	10.4
Water-Scavenger Beetles (Hydrophilidae)	18.2	9.2
Short-horned Grasshoppers (Acrididae)	12.7	6.0
Dragon-Flies and Damsel-Flies (Odonata)	28.1	5.5
Ground-Beetles (Carabidae)	22.4	3.5
Caterpillars and Moths (Lepidoptera)	24.0	3.3
Meadow Mouse (*Microtus ochrogaster*)	1.3	3.0
Birds and Feathers, Unclassified	1.1	2.2
Snails (*Physa* sp.; *Planorbis* sp.; *Polygyra* sp.)	16.5	2.1
Bluegill (*Lepomis macrochirus*)	0.4	2.1
Toad, Unclassified	0.4	2.0
May- and Dung-Beetles (Scarabaeidae)	9.0	1.9
Spiders (Arachnida)	14.7	1.2
Diving-Beetles (Dytiscidae)	4.8	1.1
Snapping Turtle (*Chelydra serpentina*)	0.4	1.0
Water-Bugs (Belostomatidae)	4.4	1.0
Fathead Minnows (*Pimephales promelas*)	0.4	0.4
Undetermined Animal Matter	3.5	0.4
Millipedes (Diplopoda)	7.9	0.4
Earthworms (*Lumbricus terrestris*)	0.9	0.3
Golden Shiner (*Notemigonus crysoleucas*)	0.2	0.3
Field-Crickets (Gryllidae)	2.2	0.2
Water-Scorpions (Nepidae)	1.3	0.1
May-Flies (Ephemeridae)	3.3	0.1
Horse-Flies (Tabanidae)	0.9	0.1
Mole-Crickets (Gryllotalpinae)	0.7	0.1
Long-horneed Grasshoppers (Tettigoniidae)	0.7	0.1
Cockroaches (Blattidae)	1.1	0.1
Snake, Unclassified	0.2	0.1
Terrapin (*Terrepene* sp.)	0.2	0.1
Fireflies (Lampyridae)	2.0	0.1
Walking-Sticks (Phasmidae)	0.7	0.1
Bumble Bee (Bombidae)	0.2	0.1
Honey-bees (Apidae)	1.1	trace
Clams (Pelecypoda)	0.9	trace
Beetles, Unclassified (Coleoptera)	3.7	trace
Blister-Beetles (Meloidae)	1.5	trace
Click-Beetles (Elateridae)	1.8	trace
Flies (Diptera)	2.0	trace
Snout-Beetles (Curculionidae)	2.2	trace
Insects, Unclassified (Insecta)	3.1	trace
Long-horned Beetles (Cerambycidae)	0.7	trace
Darkling Beetle (Tenebrionidae)	0.2	trace
Stink-Bugs (Pentatomidae)	1.3	trace
Water-Striders (Gerridae)	3.5	trace
Caddis-Flies (Trichoptera)	1.1	trace
Whirligig-Beetle (Gyrinidae)	0.2	trace
Black Bass (*Micropterus salmoides*)	0.2	trace
Crane-Fly Larva (Tipulidae)	0.2	trace
Lacewing-Flies (Neuroptera)	0.4	trace
Wasp (Sphecidae)	0.4	trace
Stone-Fly (Plecoptera)	0.4	trace
Carrion-Beetle (Silphidae)	0.2	trace

TABLE 2. (Continued)

Food Item	Per Cent by Occurrence	Volume
Soldier-Beetles (Cantharidae)	1.1	trace
Harvestmen (Phalangida)	0.4	trace
Leaf-Beetles (Chrysomelidae)	0.7	trace
Wasps and Bees, Unclassified (Hymenoptera)	1.3	trace
Water-Boatmen (Corixidae)	1.5	trace
Ants (Formicidae)	0.9	trace
Sow-Bugs (Isopoda)	0.4	trace
Velvet-ants (Mutilidae)	0.2	trace
Centipedes (Chilopoda)	0.4	trace
Leech (Hirudinidae)	0.2	trace
Squash-Bug (Coreidae)	0.2	trace
Alder-Fly (Sialidae)	0.2	trace
Tree-Hoppers (Membracidae)	0.4	trace
Sawflies (Tenthridinidae)	0.4	trace
Braconids (Braconidae)	0.7	trace
Back-Swimmers (Notonectidae)	0.4	trace
Assassin-Bug (Reduviidae)	0.2	trace
Lygaeid-Bug (Lygaeidae)	0.2	trace
Leaf-Hopper (Cicadellidae)	0.2	trace
Lady-Bugs (Coccinellidae)	0.4	trace
Syrphus-Fly (Syrphidae)	0.2	trace
Burrower-Bug (Cydnidae)	0.2	trace
? Nematode, Unclassified	0.2	trace
Crawling Water-Beetle (Haliplidae)	0.2	trace
Bugs, Unclassified (Hemiptera)	0.7	trace
Rove-Beetle (Staphylinidae)	0.2	trace
Aphids (Aphididae)	0.4	trace
PLANT FOODS		
Vegetation and Leaf Materials, Unclassified	31.1	1.8
Algae	8.8	0.5
Grass	7.7	0.2
Willow Leaves (*Salix* sp.)	2.0	0.2
Duckweed (*Lemna* sp.)	2.4	0.1
Cat-tail (*Typha latifolia*)	1.5	0.1
Brome-Grass (*Bromus* sp.)	2.4	0.1
Post-Oak Acorn (*Quercus stellata*)	0.2	0.1
Water-Flaxseed (*Spirodela polyrhiza*)	0.9	0.1
Pondweed (*Potamogeton* sp.)	1.3	trace
Barnyard-Grass (*Echinochloa crusgalli*)	1.5	trace
Spike-Rush (*Eleocharis* sp.)	1.3	trace
Wild Plum (*Prunus americana*)	0.2	trace
Cockebur (*Xanthium* sp.)	0.2	trace
Spike-Rush (*Eleocharis obtusa*)	0.9	trace
Korean Lespedeza (*Lespedeza stipulacea*)	1.5	trace
Lanceleaf Ragweed (*Ambrosia bidentata*)	0.7	trace
Rice-Cutgrass (*Leersia oryzoides*)	0.9	trace
Water-Smartweed (*Polygonum punctatum*)	0.2	trace
Sedges (*Carex* sp.)	1.1	trace
Clover (*Trifolium* sp.)	0.4	trace
Great Ragweed (*Ambrosia trifida*)	0.2	trace
Wild Rye (*Elymus* sp.)	0.2	trace
Beggar-ticks (*Bidens* sp.)	0.4	trace
Sycamore (*Plantanus occidentalis*)	0.4	trace
Oats (*Avena sativa*)	0.2	trace

TABLE 2.—(Continued)

Food Item	Per Cent by Occurrence	Volume
Panic-Grass (*Panicum* sp.)	0.2	trace
Buttonweed (*Diodia teres*)	0.2	trace
Awn-Grass (*Aristida* sp.)	0.2	trace
Common Smartweed (*Polygonum Hydropiper*)	0.4	trace
Arrowhead (*Sagittaria latifolia*)	0.2	trace
Old-witch-Grass (*Panicum capillare*)	0.2	trace
Nodding Smartweed (*Polygonum lapathifolium*)	0.2	trace
OTHER MATERIAL		
Gravel	0.7	0.1
TOTAL		100.0%

DISCUSSION

Data presented in the preceding tables provide a key to the seasonal feeding habits of bullfrogs in Missouri. A total of 82 animal and 33 plant food groups were identified in the stomach contents, but only a few animal foods and unclassified vegetation comprised as much as 1.0 per cent each, by volume, in the total diet.

Insects, as a group, comprised the major source of bullfrog foods. One or more kinds of insects were found in 83.5 per cent of the stomachs examined, and made up a combined total of 32.6 per cent of the entire volume of food. Most insects were identified to family, a few only to order. The 58 recognized groups are listed in table 2. Only eight of these groups were important in the year-around diet. Dragon-flies and damsel-flies (Odonata), especially in the nymph stage, were the second most important food during their period of emergence in May, when these insects made up more than one-fifth (20.4%) of the monthly diet. Nymphs and adults were found in lesser amounts during the summer months. Ground-beetles (Carabidae) proved to be an important food from May until October, with greatest utilization during June, when they comprised 8.0 per cent of the diet. Scarab-beetles (Scarabaeidae), principally May-beetles (*Phyllophaga* spp.), also were most heavily utilized during June, but were an important food from May through September. Several of these beetles often were consumed as part of one meal; as many as eight were found in a single stomach. Caterpillars and moths (Lepidoptera—for the most part unclassified, but including the families Pyralididae, Noctuidae, and Olethreutidae) were found in bullfrog stomachs from April through October. They were consumed with greatest frequency and volume during July, when lepidopterous insects comprised 9.2 per cent of the diet, by volume. Water-scavenger beetles (Hydophilidae) constituted a major source of food during each month, except June. This group of insects made up more than one-fourth (25.5%) of the food consumed during August. Short-horned grasshoppers (Acrididae) first appeared in the stomachs in July; showed increased importance during August; comprised more than two-thirds (67.2%) of all foods in September; and constituted the second most important item in October, to be surpassed only by crayfish. Diving-beetles (Dytiscidae) and water-bugs (Belostomatidae) also were important foods, and comprised 1.1 and 1.0 per cent, respectively, of the average diet. The remaining 50 insect foods were

relatively unimportant, since they were taken infrequently or in small amounts. Additional details on insect consumption are given in tables 1 and 2.

Crayfish (*Cambarus* spp.) comprised the second most important food group. This item occurred in 107 (23.5%) of the samples, and accounted for 26.4 per cent of all food consumed. This is almost the exact amount reported by Penn (1950). Crayfish were a major source of food each month, with the smallest amounts taken during April and September. The April diet was heavily supplemented with insects and tadpoles, which may account for the decreased utilization of crayfish then. The September figure probably was affected by the small number of samples examined (17) and by the ease with which grasshoppers could be obtained.

Frogs (all species) comprised the third most important source of food. They occurred in 37 stomachs and made up an average of 11.1 per cent of the total volume of foods. Most of the frogs eaten were unclassified, but a few were tentatively identified as young bullfrogs, and one was a leopard frog (*Rana pipiens*). Frogs as large as six inches in length were found in the bullfrog stomachs. They constituted an important portion of the stomach contents each month, except September, with greatest amounts during August and October.

Tadpoles (unclassified) occurred in 61 samples distributed throughout the year. Greatest utilization was during the month of May, when tadpoles comprised more than one-fourth (26.7%) of all food consumed. This item, during the two-year period, averaged 10.4 per cent of the total diet, by volume.

The meadow mouse (*Microtus ochrogaster*) must be classed as an important food, by volume, because of the large bulk taken at a single feeding. Actually only six mice were found in the 455 stomachs examined, but the volume of these amounted to 3.0 per cent of all food. It could not be ascertained whether these were taken from the shore or from the water, but the number of occurrences would indicate that the taking of mice by frogs is more than accidental or rare. All mice taken were full-grown or nearly so, and one was a pregnant female. The literature contains other references of full-grown mice being found in bullfrog stomachs (Palmer, 1908; Hewitt, 1950).

Fish were found infrequently in the stomach contents and occurred in only six specimens. Two stomachs contained bluegill (*Lepomis macrochirus*), two contained fathead minnows (*Pimephales promelas*), and one each contained golden shiner (*Notemigonus crysoleucas*) and black bass (*Micropterus salmoides*). One frog apparently had a predilection for fish, since its stomach contained nine bluegill, all more than one inch in length, which totalled 27.0 cubic-centimeters of food. Other occurrences were one or two fish along with other food. On the average, fish made up 2.9 per cent, by volume, of the bullfrog diet during the two-year period.

Birds were listed among the important foods only because of the large bulk of a single feeding. A fledgling songbird, tentatively identified as red-winged blackbird (*Agelaius phoeniceus*), made up a bulk equivalent of 2.2 per cent of the volume of all foods. Four additional occurrences of feathers probably were ingested without a bird having fallen prey to the bullfrogs concerned. Another local case of a fledgling bird found in a bullfrog stomach was called to the attention of the senior author during preparation of this paper. The latter, too, was tentatively identified as a fledgling red-winged blackbird.

Snails of three kinds were common items in the stomach contents and

were found in 71 samples. These comprised a combined volume which amounted to 2.1 per cent of the diet. Most common were the tadpole snails (*Physa* sp.), although wheel-snails (*Planorbis* sp.) made up a greater bulk. The common land-snail (*Polygyra* sp.) was found only once.

Toad (unclassified) was identified only once, but was of sufficient size to constitute 2.0 per cent of the volume of all foods. The question arises whether toads are less acceptable than are frogs for food. Perez (1951) working in Puerto Rico found that bullfrogs were not preying upon small toads imported for control of the sugar cane-borer.

Miscellaneous invertebrates, including spiders, millipedes, earthworms, harvestmen, sow-bugs, centipedes, and leeches were found in a total of 99 samples and made up 1.9 per cent of the diet. Spiders of several kinds made up the greatest portion of this group of foods, and were found each month from April through October. Millipedes were taken in small amounts during the spring and summer months, but in greatest quantity during October. Other items in this group were taken in insignificant amounts.

Snapping turtles (*Chelydra serpentina*) were found in two stomachs and made up 1.0 per cent of all food, by volume. Both turtles, about the size of a half-dollar, were found in specimens collected during May.

Plant materials of many kinds, for the most part unclassified vegetative parts, leaf fragments, and filamentous algae, were found in 245 (53.8%) of the stomachs examined. The combined bulk of all plant parts comprised 3.0 per cent of the stomach contents. The nature of the vegetative parts found makes it seem probable that most of such materials were taken accidentally with animal foods. Aside from filamentous algae which was present in many ponds, plant fragments most commonly consisted of stem or leaf parts of terrestrial herbs, shrubs, and grasses in small amounts. A detailed listing of identified plant materials is shown in table 2.

Dickerson (1931) stated, "The Bullfrog will eat any moving object that he can swallow or partially swallow." Such voracious feeding is verified by this study, with certain exceptions. Water-scorpions (Nepidae), water-boatmen (Corixidae), and back-swimmers (Notonectidae) were locally abundant in ponds where frogs were collected, yet rarely were found in the stomach contents. All other water insects appeared to be readily acceptable to frogs. In general, the results of this study show that bullfrogs feed upon animal foods most readily available to them, whether aquatic or terrestrial.

SUMMARY

Data were obtained from the examination of 455 stomachs of bullfrogs collected from farm ponds between the inclusive dates, April 11, 1950, to October 21, 1951.

Bullfrogs for study were obtained by hand-grabbing, by gigging, or by shooting with a .22 caliber rifle and shot-shells, in each case aided by a strong light.

Food habits data were obtained for almost the entire period that bullfrogs were out of hibernation in Missouri (March through October).

The data, presented as monthly and seasonal percentages, revealed definite changes in feeding habits throughout the year. Principal foods consumed closely parallel availability, with noted exceptions.

A total of 82 animal and 33 plant foods were identified in the stomach contents.

Principal foods, by major group, with percentages by volume, were as follows: Insects, 32.6%; crayfish, 26.4%; frogs, 11.1%; tadpoles, 10.4%; meadow mouse, 3.0%; fish, 2.8%; birds, 2.2%; snails, 2.1%; toad, 2.0%; miscellaneous invertebrates, 1.9%; and snapping turtle, 1.0%.

Plant materials, consisting mainly of unclassified vegetative parts, leaf fragments, and filamentous algae, were found in 53.8 per cent of the stomachs examined, and comprised 3.0 per cent of the total volume of stomach contents. Plant materials, nevertheless, were considered to have been taken accidentally with animal foods.

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The Population Dynamics of the Cliff Frog, Syrrhophus Marnocki

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The importance of animal population studies is emphasized in the numerous recent definitions of the species concept, most of which are expressed in terms of populations, or of groups of populations. The qualitative approach to population study influenced the theories of earlier workers such as Darwin and Wallace (1858), Darwin (1859) and Wallace (1881). Pearl (1925, 1930, 1937) and his associates were among the first to utilize biometrical methods in population studies.

The work of Wright (1940a, b, 1943, 1946, 1948, 1949) emphasizes quantitative genetic structure of natural populations, the rate of gene flow, genetic shift, and population structure in organic evolution.

Mammals, birds, fishes, insects, and plankton are most frequently studied with respect to natural populations (*Allee et al*, 1949). Studies on the various phases of the population dynamics of terrestrial vertebrates have been pioneered by a few workers: Howard (1949), Blair (1950), Burt (1940) and others in mammals; Cagle (1944), Stickle and Cope (1947), Stebbins (1948) and others in reptiles; Breder, Breder and Redmond (1927), Bogert (1947), Stebbins (1949), A. P. Blair (1941a, b) and others in amphibians. Work on movements of individuals in amphibian populations has been concerned mostly with breeding aggregation, homing instinct, or responses to drought.

The terrestrial life histories of certain amphibians lend themselves well to the study of population dynamics. Species of amphibians with an entirely terrestrial life history occur in 10 of the 13 or more families of salientians (Orton, 1947). However, only four such terrestrial frog species are found in the United States. These include two genera of the Leptodactylidae. The species are *Eleutherodactylus ricordi, E. latrans, Syrrhophus marnocki* and *S. campi.* Such amphibians are perhaps a curiosity to the North American worker because of their rarity and limited distribution on this continent.

The present account adapts both the standard techniques of life history studies in amphibians and those techniques used in the study of the structure of small mammal populations to one of these species, the cliff frog (*Syrrhophus marnocki* Cope), which occurs rather commonly in the mountainous portions of central and west Texas and northern Mexico.

The local variation, population structure, home range, environmental relations and breeding behavior were studied in order to estimate the importance of these factors on the potential and the rate of spread of mutant characters through the populations.

Acknowledgments.—The writer wishes to express his indebtedness to Mr. Alvin G. Flury for suggesting and helping with the early phases of this problem. The active interest and assistance in the field problems shown by Dr. W. F. Blair are deeply appreciated. Dr. J. A. Cairns has given valuable assistance with the laboratory methods. Dr. Clark Hubbs has offered many helpful suggestions about the statistical methods and presentation

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METHODS

Field techniques were utilized that would demonstrate environmental relations, population structure, and breeding behavior of the amphibian populations. At 12 Travis County localities, 255 cliff frogs were marked, released, and recaptured in order to obtain estimates as to the sizes of the populations, the changes or turnover of the individuals in the populations, the variations in the population densities, sex ratios, migrations and movements of the adult individuals, dispersal of juveniles, and estimates of the sizes and variations of sizes of home ranges.

The cliff frogs were marked by toe clipping of the forefoot. The method was adapted from that of Blair (1941) and is demonstrated in the following table where the symbol (1) represents an entire toe, the (0) a clipped toe:

RIGHT HAND		LEFT HAND	
0111	1	0111	10
1011	2	1011	20
1101	3	1101	30
1110	4	1110	40
0110	5	0110	50
0011	6	0011	60
0101	7	0101	70
1010	8	1010	80
1100	9	1100	90

The chief value of this method was that one could mark up to 99 frogs using only the forefeet. Only the anterior appendages were used because a count of the present and missing front toes could frequently be made without the necessity of capturing the individual or disturbing its activity. Only three individuals of more than 800 collected for breeding experiments and local variation studies were found to lack a toe. Thus confusion of numbers due to accidental loss of a toe is believed to be very slight. There was apparently no regeneration effect sufficient to obscure the marking. It is believed that there was probably little effect of the marking technique on survival of individuals.

Measurement of the snout-vent length of each individual was made during the study, usually at the first observation of a given individual in each season. The position of the frog, with reference to the nearest rock, was recorded for each observation. The under surface of the rock was numbered with pencil so that a more or less permanent record was available at the locality. The tops of the rocks were marked with soft red pencils so that they could be easily found in the daytime when the maps were brought up to date. Additional notations on the sex, presence of eggs in the females, and feeding

observations were recorded in the field notebook. The sexing of individuals in the field was very difficult because of the absence of secondary sexual characters. The presence of eggs in the abdominal cavity during the breeding season established the sex in the case of the females. These eggs can be readily observed through the body wall. No field method was developed to tell the difference between males and eggless females. There is little doubt that some of the frogs that were considered to be males were really females.

Several field population experiments were attempted. Marked cliff frogs were released on May 22, 1951 (25 individuals) and June 9, 1951 (25 individuals) on a low bluff at Clark Field near the University of Texas campus. No individuals of *Syrrhophus* had previously been found at this locality in 1948, 1949, or 1950. The movements of the frogs over this virgin bluff were recorded. Twenty-five marked individuals were released within the area of a previously marked population on September 9, 1951. The movements of these new individuals and their effect on the resident population were recorded. Frogs were marked in the area around a bluff at Mount Bonnell from May 1 to May 25, 1951. From May 25 until June 15, all individuals found along the bluff were removed. The movement of marked frogs from the surrounding area into this area of induced low population density was recorded.

Population samples from nine localities in Travis County, two in Williamson County, and one in Hays County were collected and preserved. Several measurements were made on each individual in the Texas Natural History Collection, A. G. Flury collection, the F. E. Potter collection, and on the 12 population samples. These measurements were designed to determine whether or not morphological differences exist between different local populations.

The extension of small mammal field techniques to amphibian populations will perhaps stimulate additional use of the methods in other cold-blooded vertebrates. Various modifications of the "standard" mammal techniques were necessary for this study. No doubt further adjustments will be necessary as other groups are studied. The new methods forced upon later workers by the inherent structure of the various population types should result in an increased efficiency of the overall technique and in greater respect for the potentialities of the procedure.

ENVIRONMENTAL CONDITIONS

CLIMATE

The general climatic conditions of South Central Texas are greatly affected by the prevailing southerly winds resulting from the nearness of the Gulf Coast and the Tropics. Polar influence results in prevailing northerly winds only in December, January, and February. The mean annual temperature in Travis County is 67.6° F. The winter daily range averages 40° to 60° F, but sudden changes may result from the interaction of polar and tropical air masses. The summer daily range averages from 74° to 90° F. The maximum and minimum recorded temperatures are 106° and -2° F. The growing season is 263 days.

The annual precipitation over 50 years has varied from 16 to 65 inches, with the average of 34.08 inches. There are no distinct dry and wet seasons,

rainfall being fairly well distributed throughout the year. Extensive droughts occur with some frequency. The annual precipitation for the six years of the study is as follows: 1946—47.28 inches; 1947—21.58 inches; 1948—20.98 inches; 1949—36.34 inches; 1950—25.79 inches; 1951—28.98 inches. The period during which this work was done demonstrates approximately six inches of subnormal precipitation.

EFFECTS OF WEATHER ON ACTIVITY

Weather conditions are important factors in the ecology of any wild population. Unfortunately these factors are difficult to study, and adequate conclusions are not always obtained from the data. In an attempt to resolve the effect of certain of these factors on the activity of *Syrrhophus*, an experimental transect was established as a measured line of 100 yards along the base of a small bluff (Washita group: Buda overlying Del Rio). This transect was walked 392 times in 1949, 1950, 1951, and the number of individuals heard or seen was counted. A marked population was not used in order to avoid errors produced by disturbance of the individuals. The path was cleared of rocks and debris so that the transect could be walked as quickly as possible. Five minutes were spent on each walk. The assumption was made that the number of frogs calling represented a sample of the number of frogs active at a given time.

The peaks of *Syrrhophus* activity along this transect were in April-May and September-October, 1949; late April-early May and September, 1950; late May-early June and September, 1951. The temperature in these months ranged from 63.5° to 79.2° F. The fall activity peaks came at slightly warmer temperatures than those temperatures found during the spring peaks of activity. The rainfall for these months ranged from 3.51 to 7.58 inches. Assuming an equitable distribution of annual rainfall (34.08 inches) for each of the 12 months, the average monthly rainfall would be 2.84 inches. Every month during the peak of frog activity had more rainfall than this theoretical average. The maximum activity was found to occur in April in both 1949 and 1950, coinciding with the spring rains of those years. The rains of 1951 were late, and the peak of activity of the frogs was delayed until late May and early June.

The relative temperature rather than the absolute temperature may play a leading role in the initiation of the breeding activity. In January and February when lower temperatures are normal, if the temperature rises after a drop produced by a polar front, the frogs are often rather active.

Of the 392 observations, 273 were made at relative humidities from 76-100 percent. The frogs are more active when light intensities and wind strength are low. Some ground moisture is necessary to support activity in these amphibians, but excessive moisture, as observed on six occasions, apparently curtailed the activity of the frogs. On these nights it had rained, or was raining so hard that water actually flowed in streams on the very tops of the bluff over the transect. On these same nights there was a curtailment of *Syrrhophus* activity in all localities visited. It should be pointed out that the several nights following these flooding rains were ones on which some of the most intensive cliff frog activity was observed. This curtailment of frog activity when ground moisture reaches saturation may be attributed to the

absence of any swimming ability in these frogs. Individuals of this species will drown in one to two hours when placed in a jar of water.

The effect of the weather on activity of the cliff frogs can perhaps be emphasized by the difference in the activity of the individuals under various conditions. In very cold, wet weather (40-50° F), individuals of *Syrrhophus* were observed for several successive nights in the same protected crack in a bluff; they moved sluggishly back into the cracks when disturbed. In the spring and fall and during the summer rains, the frogs were seldom recovered in the same small area on consecutive nights, and their movements were so quick as to make it very difficult to capture more than 75% of the individuals observed.

Individuals were found when temperatures were excessively low (34° F) or high (91° F). On occassions they were found when the relative humidity was as low as 35% and when the wind was sufficiently strong to drive along dust, sand, and rocks. Individuals were found (September 17, 1950–January 10, 1951) when there had been only 1.37 very scattered inches of rain in 147 days. One individual has occasionally been heard from under the steps of the author's house through the fall of 1951 calling in daylight (10 a.m.–3 p.m.) at temperatures from 56° to 82° F. with the sun brightly shining.

A combination of interrelated weather conditions is responsible for the number of males that call. If the assumption that the number of males observed calling represents a sample of the number of frogs active is accepted, then it is apparent that the activity of the frogs is related to several weather variables (temperature, relative humidity, ground moisture, light intensity, and wind).

TIME OF ACTIVITY

The cliff frogs were most active in the hours shortly following dusk. When weather conditions were unfavorable, these amphibians were seldom observed after one or two a.m. The weather conditions that prevailed during the breeding season were apparently conducive to longer hours of activity. In the spring and fall, individuals were heard calling around the writer's residence from dusk until just after dawn. Occasional individuals have been heard calling in the daytime from moist places under houses and in caves.

GEOGRAPHY, TOPOGRAPHY, AND PHYSIOGRAPHY

A considerable portion of the work was done in Travis County where the Colorado River crosses the Balcones escarpment. The county is located along the transition zone between the Edwards Plateau of West Central Texas (Edwards Plateau: Tharp, 1939; Balconian biotic province: Blair, 1950a) and the blackland prairie of the coastal plain (Blackland Prairie: Tharp, 1939; Texan: Dice, 1943, Blair, 1950a). The southern and eastern edges of the Edwards Plateau (Comanche series, lower Cretaceous) are heavily dissected and mountainous, rising to 1300 feet elevation in Travis County. The blackland prairie (Gulf series, upper Cretaceous) consists of rolling grasslands ranging in the county from 400 to 600 feet elevation.

The geology of this region is complicated by the Balcones faults, which produce a line of separation between the lower and upper Cretaceous. North

and west of the Balcones escarpment the lower Cretaceous (Comanche series) consists of the Trinity group (Glen Rose, Travis Peak), Fredericksburg group (Edwards, Comanche Peak, Walnut) and Washita group (Buda, Del Rio, Georgetown). The upper Cretaceous is a series of southeast dipping formations whose strike runs northeast—southwest. The geologic groups of the Gulf series and their Central Texas formations are as follows: Colorado group (Austin, Eagle Ford), Montana group (Navarro, Taylor).

Trinity Group.—The Glen Rose formation, with its alternating hard and soft limestone, which produces terraced hills of relatively infertile soils, supports abundant cedar (*Juniperus mexicana*), *Rhus*, scattered white oak (*Quercus durandi*) and grasses including *Muhlenbergia, Bouteloua hirsuta, Andropogon scoparius,* and *Triodia elongata.* Here, the cliff frog populations (Mount Bonnell, Lake Austin Park, Gaines Ranch, Farmer's Ranch) were easily studied and usually abundant. Small caves (Balcones Cave) in this formation often supported large populations. The Travis Peak formation apparently erodes too finely to support cliff frog populations, although individuals of this species are occasionally found when the Travis Peak formation is associated with the Glen Rose rocks.

Fredericksburg Group.—The Edwards formation consists of hard crystalline limestone. It erodes to black and chocolate soils which support dense live oak (*Quercus virginiana*) and scattered cedar (*Juniperus mexicana*) with *Aristida purpurea, Buchloe dactyloides, Andropogon scoparius* and other grasses. Along the bluffs near streams and around hill caps, the Edwards supports considerable populations of *Syrrhophus* (Boy Scout Hut, Oak Hill). Additional large populations are supported near the cave openings and within many of the caves, both small (Merrell's cave) and extensive (Steam cave, Ezelles' cave) which are formed in these rocks. The Comanche Peak and Walnut formations, both of which support Spanish oak (*Quercus texana*) and ash (*Fraxinus texana*), are apparently without populations of *Syrrhophus*. Possibly these rocks are too chalky and erode too finely to provide adequate cover for these frogs. Where the Walnut formation was found in association with the Glen Rose, occasional individuals were discovered.

Washita Group.—The Buda, which supports elm and hackberry, consists of massive crystalline limestone overlying the marly and soft Del Rio and often erodes into small talus slopes which fall on the lower slopes of the Del Rio Formation. Cliff frogs are abundant (Lamar Boulevard in Austin) both among the talus rocks and in and around the weathered exposures of the formation. However, the cliff frog has not been found on the Del Rio except where the Buda stones were scattered over its surface.

The soft nodular limestone of the Georgetown erodes to black soils forming prairies with scattered but common *Juniperus mexicana* and *Rhus aromatica* var. *serotina* and *Diospyros texana.* In the natural erosion of this formation little cover is provided for these frogs, but occasional individuals have been found around road cuts.

Colorado Group.—The Eagle Ford, consisting mostly of dark gray and black shales with little vegetation other than occasional mesquite and hackberry apparently is not populated by *Syrrhophus.* The Austin Chalk, con-

sisting of massive chalky limestone, which weathers to fertile black soils supporting live oak (*Quercus virginiana*), elm (*Ulmus crassifolia*), and hackberry, (*Celtis mississippiensis*), provides in many places ample shelter for the cliff frog (Onion Creek, Onion Quarry, Waters' Park, and the University of Texas campus). However, apparently excellent localities for these frogs (the outfield wall of the University of Texas baseball park, some areas around Memorial Stadium) were apparently without cliff frog populations. The absence of frogs in these latter two localities is discussed elsewhere.

Montana Group.—The Navarro and Taylor formations, characterized by their black soils, rolling grasslands (*Andropogon, Bouteloua, Triodia*), mesquite (*Prosopis glandulosa*), post oak (*Quercus stellata*), blackjack oak (*Q. marylandica*), and frequently prickly pear (*Opuntia lindheimeri*) offer very little of the rock outcrop to which *Syrrhophus* is apparently limited, and no individuals of the species have been taken on these formations.

Nowhere in the natural habitat have *Syrrhophus* been found in sandy situations. However, in the artificial habitat of gardens, around leaky faucets, and under houses where scrap rock, debris, etc. are available for shelter, these frogs frequently occur during the summer months. It is safe to assume that the frogs are seeking the moisture rather than the sandy soil of the gardens.

Thus we see that the distribution of individuals of *Syrrhophus* is closely associated with the geologic strata and apparently correlated with the lithology and physiography of the various formations. It is apparent that the formations supporting abundant cliff frog populations are those that weather, at least on stream banks, bluffs, and steep slopes, to smaller and yet massive rocks, which in turn break down into soil. Those formations that are distinctly marly or shady do not as a rule support *Syrrhophus,* apparently because weathering is more directly from thin bedded marls and shales to overlying soils. In some cases the general topography or road and building construction may influence the weathering of some of these forms in such a way that there is a breakdown to more massive blocks; apparently this has occurred in some of the Austin Chalk exposures. Considerable observation indicates that the amount of rock surface exposed by the varying processes of weathering plays an important role in the variation of population density and in the size of the home range of the individuals that make up the populations.

The factors that directly limit the presence or absence of the cliff frog on a given formation are unknown. The cover provided by the greater surface of the more massive rocks (Austin, Buda, Edwards, Glen Rose formations) may account for the greater abundance of cliff frogs on these formations. Also it may be well to point out that these more massive formations frequently tend to sweat on hot summer nights, whereas those formations that weather to fine clays, sands, and tight blacksoils (Navarro, Taylor, Eagle Ford, Woodbine, Del Rio, Georgetown, Comanche Peak, Walnut, and Travis Peak) tend to absorb rather than give off air moisture.

HABITAT

Very few workers have commented on the habitat preferences of the cliff frog. Gaige (1931) reported these frogs from around rocks in the vicinity of creeks in the Chisos Mountains. Schmidt and Smith (1944), Strecker (1930),

Strecker and Williams (1927), and Marr (1944) mentioned the cliff frog as saxicolous. Mohr (1949) and Nicholson (1932 a and b) reported its occurrence in caves. Jameson and Flury (1949) reported *Syrrhophus* from the stream bed, catclaw-grama, and rock bluff associations of the Roughland life belt in the Sierra Vieja biotic district. They did not find it in the Plains life belt. Milstead, Mecham, and McClintock (1950) found the cliff frog occasionally in the live-oak and persimmon-shinoak associations but predominantly in the cedar-oak association of the Stockton Plateau biotic district.

From the present study two additional habitats can be added to those in which the cliff frog is found. On four occasions individuals have been found on limbs from five to eight feet high in live oak trees (*Quercus virginiana*). On one occasion a cliff frog was found on the limb of a hackberry tree (*Celtis mississippiensis*) about four feet above the ground, and once one was found about six feet high on a greenbriar (*Smilax bona-nox*). These arboreal activities were noted only during the height of the breeding season, following heavy rains, with the humidity from 90–100% and the temperature from 68–76° F.

DESCRIPTION OF THE HOME RANGE LOCALITIES

The geology, physiography and major vegetational features of the 12 localities where cliff frogs were marked are indicated in table 1. Eight of the localities are on Glen Rose, one on Edwards, one on Buda, and two on Austin Chalk.

Three of the localities are more or less isolated cliffs surrounded by open cedar breaks, grasslands, or generally non-rocky topography. No other cliffs or talus are present within the normal range of movement of the adult frogs. The five cliff localities are segments of outcropping rock in various stages of weathering. These localities are along dissected creeks and rivers where the terraces below, and the cedar breaks, grasslands, and deeper soils above, serve as partial barriers to the movement of the frogs. These cliffs vary from three to eight feet high.

Mount Bonnell No. 2 is an artificial talus slope found below a road constructed along the face of a bluff. The steep slope is characterized by rocks six to 24 inches in diameter, which provide excellent shelter for the frogs.

The two open slope localities are characterized by minor terraced outcrops of rock from six to 24 inches in thickness. These rock outcrops are from 20 to 60 feet apart with scattered cedars and grasses in the intervening soil.

The Farmer's Ranch locality is an abandoned stone quarry consisting of the open rock face of the quarry on one side and the scrap stone opposite and parallel about 40 feet away. The scrap stone is of varying size, but a considerable portion of it contains stones from three to six feet in diameter.

None of the localities used in this study is entirely cliff, talus or open slope, as each physiographic condition is present at most of the localities. The indicated physiographic type represents only the dominant condition at the locality.

FOOD RELATIONSHIPS

Several vertebrates (encinal mouse, broad-striped skunk, armadillo, ring-necked snake, ground snake, barking frog, Mexican toad, canyon toad) and

TABLE 1.—Size of home range of possible males during the breeding season.

Locality	Number of Frogs	Average Number of Observations	Size in Home Range in Acres	Geology	Physiography	Major Vegetation
Lake Austin Park	16	6.00	0.154 ± .010	Glen Rose	Open Slope	Cedars
Mount Bonnell No. 1	17	6.00	0.173 ± .014	Glen Rose	Open Slope	Cedars
Farmer's Ranch	76	8.01	0.108 ± .005	Glen Rose	Quarry	Cedars
Bee Caves No. 1	2	4.00	0.075 ± .015	Glen Rose	Cliff	Cedars
Bee Caves No. 2	2	4.00	0.090 ± .000	Glen Rose	Cliff	Cedars
Mount Barker	20	8.50	0.101 ± .010	Glen Rose	Cliff	Cedars
Westview	34	6.59	0.085 ± .004	Glen Rose	Cliff	Cedars
Boy Scout Hut	21	6.76	0.118 ± .007	Edwards	Cliff	Live Oaks
Lamar Boulevard	26	11.70	0.105 ± .017	Buda	Cliff	Hackberries
Waters' Park	7	4.59	0.081 ± .009	Austin Chalk	Cliff	Live Oaks Hackberries
Onion Creek	7	6.00	0.099 ± .019	Austin Chalk	Cliff	Live Oaks Hackberries
Mount Bonnell No. 2	19	5.89	0.066 ± .005	Glen Rose	Talus	Grasses

orbit web-spiders, which are found in the *Syrrhophus* habitats, are thought to be competitors with cliff frogs for food.

The diamond-back rattlesnake, the copperhead, the garter snake, and large wolf spiders are known predators on the frogs in the natural environment. The barking frog, Mexican toad, and tarantula have been observed to feed on cliff frogs in the laboratory.

Ants, small beetles, camel crickets, termites, and small spiders are known foods of the cliff frogs. Laboratory individuals feed on spiders, roaches, crickets, small grasshoppers, termites, beetles, horse flies, house flies, fruit flies, and ants. The most satisfactory method of feeding laboratory populations was to force gently small portions of animal liver into their mouths. Once the meat was in their mouths they would willingly swallow it.

Observation indicates that apparently comparable weather factors are responsible for the activity of most of the natural populations of animals found in the cliff frog habitats. This would account for the congruency of the activity of the amphibian, its food species, and many of its predators.

BREEDING, DEVELOPMENT, AND GROWTH

BREEDING SEASON

The breeding season, as indicated by the presence of eggs in the females, extended from late February to early December. The occurence of juveniles and the overall activity of the frogs indicated that most of the breeding activity occurred during the spring and fall rains. The data from collecting and from home-range studies suggested that eggs were produced and developed during hibernation of the females. In most cases females were found with eggs present on the first observations in a given season. The females apparently took little more than two to three days to mate. On no occasion was a female found to carry discernible eggs as much as one week. The same environmental factors that induced increased activity of the frogs were presumably responsible for initiation of breeding activity.

BREEDING SITES

Eggs were not found in nature despite considerable effort to locate them. Females were found on one night with eggs and again on the next night without eggs. A fair estimate of the limited area in which the eggs could have been laid was thus available. It was most disheartening to be unable to find the eggs under such circumstances. Amplexus was observed on two occasions in the field. On one occasion (April 16, 1949) a pair was found on a rock surface on the top of a cliff at Mount Bonnell. When disturbed the male released his hold, and both individuals attempted to escape. The pair was captured and brought into the laboratory where they did not mate. On May 18, 1951, a pair of frogs was found clasped in a small vertical crevice in the cliff at Mount Bonnell. There was a layer of dry dirt in the bottom of the crevice. When disturbed the pair separated and retreated into a crevice beyond sight. The crevice was visited about thirty minutes later when a pair was captured in the mouth of the crevice. They were not clasped but were assumed to be the pair previously seen. This pair was brought into the laboratory where repeated claspings and separations were observed, but no eggs were laid.

On both of these occasions when clasping pairs were found in the field the male continued to call while clasped. Males have not been observed to call after clasping in the laboratory. In neither case would the careful deposition of the eggs in moist soil have been possible, whereas eggs laid in the laboratory were carefully covered.

Males that continued to call in the field while clasping may have been attempting to lure the females to better deposition sites. This would perhaps explain why the males did not continue to call when they had clasped females in the laboratory, where moist earth was available. Another possibility is that the continued calling played a role in the deposition and fertilization of the eggs. Laboratory matings were unsuccessful and the eggs laid were sterile.

It seemed that the selection of a breeding site was dependent on the activity of the male frog. For a successful mating to occur the calling site to which the male attracted the female seemed to be one where sufficient moist soil was available for the laying of the eggs.

CALLS

Several types of calls have been heard in *Syrrhophus*. The typical cricket-like call of the cliff frog is heard throughout the year. This call can be heard up to about 100 feet. The weather factors that affect the calling have been discussed.

These amphibians demonstrate a complex social pattern similar to that described in *Eleutherodactylus latrans* (Jameson, 1954) and in *Hyla crucifer bartramiana* (Goin, 1948), in which the calls of the local individuals follow that of a leader. This leader appears to be the individual with the loudest voice in the area. This hierarchy is usually limited to three or four individuals (similar to that of *Hyla crucifer*) rather than to a dozen or more individuals as found in *Eleutherodactylus latrans*. When the local leader is disturbed, the other individuals cease to call and do not call again until the leader resumes calling.

Since these call patterns are found throughout the year and not just in or during the breeding season, it is difficult to believe that they are entirely breeding phenomena; however, their origin may be linked with the development of terrestrial breeding patterns.

Syrrhophus also has another rather strikingly different call, characterized by its rapidity, clarity, and sharpness, which is heard only during the height of the breeding season. When this call is traced to its origin, one finds either a clasping pair (the male continuing to call even when clasping) or a male with a female nearby.

MATING

Cliff frogs have been observed to court, mate, clasp, and lay eggs in the laboratory. The male approaches the female, scratches the female's back, neck, and legs with his hind leg and, if the female does not jump away, will then complete an axillary clasp. The male continues to excite the female by the use of his hind legs. The female then digs a trench with her forelegs and deposits the eggs as the pair moves along this trench. Both individuals utilize their hind legs to cover the eggs as they move, and the entire process of laying eight to 20 eggs takes little more than 20 minutes. There is no

evidence that either individual remains with the eggs. The type of embryological development has not been determined but the large-yolked eggs and the laying behavior suggest that it is similar to that described for *Eleutherodactylus* (Goin, 1947; Lynn and Lutz, 1946; Jameson, 1950).

NUMBER OF MATINGS PER YEAR

There is considerable indication that the females mate more than once each year. Marked females have been found with eggs present in the abdominal cavity in the spring and again with eggs present in the fall on several occasions. One female (No. 42—Farmer's Ranch) was found with eggs on April 9th, without eggs on April 18, with eggs on June 7th, without eggs on June 10th, and with eggs on September 11th. It is possible that this frog mated three times in 1951. The males may mate several times in one season.

PERIOD OF DEVELOPMENT

Since no eggs have been developed in the laboratory and no direct observations of development are available, the time from laying to hatching is unknown. The greatest concentration of juveniles at one time was found on August 19th and 20th, 1951, following several inches of rain. No juveniles were found previous to this in July or August. The greatest number of females with eggs was found about May 15th. This would perhaps suggest 90 days as the necessary time for development. It more probably means that the juveniles are not active after hatching until sufficient moisture is available to assure their survival.

GROWTH

The snout-length of the individuals on the home range plots at the first observation of each season was recorded. These data indicated that the frogs grew faster through the fall and winter months. It was further apparent that the rate of growth decreased as the frogs became larger.

SEXUAL MATURITY

The length at which females reach sexual maturity is from 19 to 22 mm. This is based on the lengths of females that were found with eggs. The lengths of the frogs found calling indicate that the males reach sexual maturity at from 18 to 22 mm. in length.

POPULATION DENSITY

To calculate the population density of the cliff frogs, certain adjustments must be made in the size of the area studied before we can arrive at a reliable index of the number of frogs. W. F. Blair (1941) has suggested the addition of one-half of the average home range size to those sides of the study area not bordered by barriers. This correction is designed to account for individuals whose ranges extend beyond the area observed.

Bee Caves No. 1, Bee Caves No. 2, and Mount Bonnell represent what may be considered ecological islands consisting of limestone outcrops that support abundant populations, surrounded by more eroded physiogeographies

that tend to form partial barriers to the activity of the frogs. In these cases the extremes of the home ranges were used to establish the boundaries of the area worked.

The cliffs and talus slopes of Boy Scout Hut, Mount Bonnell No. 2, Westview, Farmer's Ranch, Waters' Park, Lamar Boulevard, and Onion Creek are experimental plots that comprise segments of lengthy outcrops. These segments are bounded above by flat topography and below by terraces or creek bottoms, both of which are apparently partial barriers to *Syrrhophus* distribution. At these latter localities a strip equal to one-half the average width of the home range is added to each of the segment to account for the extension of the home range of border individuals along the outcrop.

The open slope of minor outcrops, as demonstrated by Lake Austin Park and Mount Bonnell No. 1 represent segments of a generally continuous environmental type. For these areas one-half the width of the home-range is added to each side of the segment. The adjusted sizes of the experimental plots are given in table 2.

Space, as represented by the available rock surface, and cover, as represented by the niches and crevices available to each individual and to some extent by the grass and shrub growth between the niches and crevices, are apparently the most important factors in determining the population density. Moisture is correlated with space and cover from the standpoint of the amount of plant cover available. Availability of food is obviously correlated with the above factors in that the size of the insect population is influenced by space, cover, and moisture.

There was considerable variation in the population densities in the areas worked. Population densities were found to be highest in such localities as Bee Caves No. 1 (5.3 frogs per acre), Bee Caves No. 2 (5.2 per acre),

TABLE 2.—Size of experimental plots for home-range study

Locality	Adjusted Size of Plot, in Acres	Average Size of Home Range, in Acres	Number of Average Home Range Areas on Plot
Bee Caves No. 1	.758	.075	10.1
Bee Caves No. 2	1.148	.090	12.7
Lake Austin Park	4.132	.154	26.8
Boy Scout Hut	1.745	.119	14.7
Mount Bonnell No. 1	17.906	.173	103.4
Mount Bonnell No. 2	1.010	.066	15.2
Mount Barker	1.561	.101	15.5
Westview	3.489	.085	41.2
Farmer's Ranch	7.117	.108	66.1
Waters' Park	1.332	.081	16.4
Lamar Boulevard	2.870	.105	27.3
Onion Creek	3.145	.099	31.8

Mount Bonnell No. 2 (6.9–8.9 per acre), Mount Barker (4.4–6.4 per acre), Waters' Park (4.5–5.8 per acre), and Boy Scout Hut (5.2–6.3 per acre). These localities are ones in which there are heavily dissected bluffs and talus slopes with considerable undergrowth of grasses and shrubs. The bluffs of the Farmer's Ranch locality are as greatly dissected, if not more so, than the above six. The shortage of vegetation possibly accounts for the lower population densities (3.8–4.8 per acre) found there. The Lamar Boulevard (3.1–4.2 per acre) and Onion Creek (3.5 per acre) populations have as much or more vegetation as the localities with the highest densities, but they lack the heavy dissection of those six localities. The Lake Austin Park and Mount Bonnell populations represent localities where both the vegetation and amount of dissection are very low. Here the population densities are lowest (1.21 to 2.01 frogs per acre). There was a drop in population density at Lake Austin Park from 2.42 in 1950 down to 1.69 in the spring of 1951 and 1.21 in the fall of 1951 frogs which was perhaps to some extent caused by a fire which razed the area in December of 1950.

The population densities at the Westview locality began at a rather high level (5.45 frogs per acre in the spring of 1950), but in the spring of 1951 (3.44 frogs per acre) and fall of 1951 (2.01 frogs per acre) these densities showed a marked drop. This was undoubtedly attributable to road construction and quarrying carried on in August, 1950, and from March, 1951, to January, 1952. In this interval the vegetation was destroyed, and considerable alteration in the bluffs was produced. Some of the frogs were possibly killed by the activity of bulldozers and scrapers.

There is a general tendency toward apparent higher population densities in the spring than in the fall. This could be attributed to 1) the fact that the season is shorter in the fall (three to four weeks) than in the spring (four to six weeks); 2) to the differences in precipitation and temperature and their effects on activity; 3) or to an actual change in the population densities between the spring and the fall. Each of these change factors is undoubtedly involved in producing these differences in the estimated population densities.

ESTIMATED POPULATION DENSITY ON GLEN ROSE OPEN SLOPE

In preparation for an experiment to measure the movement of frogs into an area in which the resident population had been depleted, 26 frogs were marked in the three night interval May 14–16. Of these marked frogs, 18 were recovered in the 29 frogs observed May 21, 22, and 23. The Lincoln Index can be used to estimate the total population on the 14.52 acre plot studied. The Lincoln Index is a proportional method of estimating population that utilizes the following formula (Allee *et al.*, 1949, p. 269):

$$\frac{\text{No. individuals marked precensus period}}{\text{Other individuals in precensus period}} = \frac{\text{Marked individuals captured in census}}{\text{Other individuals captured in census}}$$

or

$$\frac{26}{X} = \frac{18}{11} \quad \text{or} \quad X = 15.88 \quad \text{and}$$

the total frog population is: Number individuals marked in the precensus period + X.

Total population = 15.88 + 26 = 41.88

The total population divided by the number of acres gives a population density of 2.88 frogs per acre for the Glen Rose open slope. The estimated population densities at the two localities (Lake Austin Park, Mount Bonnell No. 1) with this physiography varied from 1.21 to 2.42 during the study. The home range studies are based on populations on somewhat more open physiographies. It is doubted that the Lincoln Index would be satisfactory for the insular localities because of the small number of frogs found in these areas.

CONCENTRATIONS OF FROGS

Blair (1951a) considered the average number of resident individuals of the same sex per average home range area as the best estimate of the amount of crowding in a population. One individual per available home range suggests unoccupied areas or even division of territory. More than one individual per available home range indicates overlapping ranges. The degree of concentration would perhaps suggest the amount of competition between individuals for food, mates, and breeding sites. Blair (1951a) maintains that the males and females do not compete and considers them separately.

The concentrations of resident individuals during the study at the 12 localities are shown in table 3. This table does not separate the males from the females. Concentrations from 0.14 to 0.74 were shown by the frogs. The highest concentrations (0.45–0.75) were found in the Boy Scout Hut, Mount Bonnell No. 2, and Mount Barker populations. The lowest concentrations (0.19-0.30) were found at the Lake Austin Park and Mount Bonnell No. 1 localities. The greatest fluctuations in concentration were found in the Westview population; these were probably caused by the losses of individuals by road construction and quarrying on the plot.

The home range study indicates that these frogs are more or less restricted

TABLE 3.—Number of resident individuals per average home range.

Locality	Total Resident Individuals				No. Per Average Home Range			
	1950		1951		1950		1951	
	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
Bee Caves No. 1	3	....	....	....	.30	....	....	....
Bee Caves No. 2	4	....	....	....	.33	....	....	....
Lake Austin Park	8	6	5	....	.30	.22	.19	....
Boy Scout Hut	9	9	11	....	.61	.61	.75	....
Mount Bonnell No. 1	31	....	....	....	.30	....	....	....
Mount Bonnell No. 2	....	7	9	9	....	.46	.59	.59
Mount Barker	9	7	8	7	.58	.45	.52	.45
Westview	17	15	12	6	.41	.36	.29	.15
Farmer's Ranch	24	29	31	25	.36	.44	.47	.38
Waters' Park	6	5	....	....	.37	.31	....	....
Lamar Boulevard	8	10	12	9	.29	.37	.44	.33
Onion Creek	10	....	....	....	.31	....	....	....

in their activity by the rock areas. The home ranges of the individuals tend to overlap on the rock areas, but they overlap very little on the open spaces between and around rock exposures. Thus competition for food and breeding sites may be considerably higher than is indicated by the above figures.

POPULATION TURNOVER

The total amount of turnover in the populations at each locality is indicated in table 4. Seven localities were observed in both spring and fall of 1950. Of 103 frogs observed at these localities in the spring of 1950, 46 were not found in the fall of 1950. This represents a 45.3% loss for the spring-summer season of 1950. Of 87 frogs observed at the seven localities in the fall of 1950, 57 were recovered in spring, 1951. This loss of 30 frogs was 34.0% for the fall-winter season of 1950-51. Only five localities were studied in both the spring and fall of 1951. Forty-one of 76 frogs (54.0%) were lost between spring and fall of 1951.

At the three localities (Mount Barker, Farmer's Ranch, Lamar Boulevard) which were studied in all four seasons the losses were greater through the summer (21 of 54—38.9% for summer, 1950 and 20 of 55—36.4% for summer, 1951) than through the winter (15 of 50—30.0% for winter, 1950-51). This may have been caused by the activity of the predators during the summer. Of the 54 frogs marked in these localities 45 (81.5%) were lost during the four seasons, which suggests that from two and one-half to three years are required for a complete turnover in the population.

Apparent or actual decrease in population numbers may be attributed to 1) dispersal of juveniles born in the study area to other areas, 2) inclusion of juveniles that were dispersing through the area in the population estimate, 3) movement of adults from the area, 4) inability of the worker to recapture females in later seasons, 5) death of individuals from marking techniques or handling, 6) death of individuals through natural injuries, 7) death of individuals because of predators. In the eight localities that were worked for more than one season 117 (47.7%) of 245 frogs were missing in later observations (table 4).

The effect of dispersing juveniles may perhaps be indicated by the number of juveniles lost in relation to the total number of losses. Of 117 frogs lost, 24 (20.5%) were juveniles. This figure (20.5%) represents both those juveniles lost through dispersal and those lost to predators. These 24 juveniles were lost from 101 marked juveniles.

The amount of movements of adults from the area is very difficult to measure. These frogs establish a home range and tend to remain at least in the same area for the life span of the individual. One would expect very few or no such movements from insular areas (Bee Caves No. 1, Bee Caves No. 2, Mount Barker). Movements of adults would be more likely in the Glen Rose open slopes where ecological conditions are apparently not the most ideal. Movements in these localities (Mount Bonnell No. 1, Lake Austin Park) would be very difficult to measure as it would be necessary to search very extensive areas. In the remaining localities, consisting of segments of cliffs, most of the adult movements would be expected to extend along the bluffs. However, none of the frogs that disappeared from the study areas were found at other positions along the cliffs or talus slopes. This is additional evidence

for the permanence of the home range. Adult movements were induced, however, by artificial depletion of the resident population. Movements might possibly have been induced in the Mount Bonnell No. 2, Farmers's Ranch, and Boy Scout Hut localities by the collection of specimens for local variation study. In these localities the time of collection coincided with the time of population structure studies. Discretion was used in the collection, however, and several hundred yards separated the collection area from the marked population.

As previously pointed out, there is probably little danger of death of the individuals because of marking techniques. Death due to natural injuries are of course possible, but few frogs were found with missing members, scars, or other marks.

Inability to recapture females in later seasons was perhaps a major source of error. Thirty-four of the 117 losses (29.1%) were females. Frogs found in one season but not recovered in the next, were not found in a later season.

TABLE 4.—Survival of cliff frogs at 12 localities from the spring of 1950 to the fall of 1951. Number of individuals marked (first number in each line), numbers recovered, and numbers lost by seasons. The number of individuals which disappeared (losses) from the plots may be obtained by subtracting the second column from the first.

Locality	1950		1951		Total
	Spring	Fall	Spring	Fall	
Bee Caves No. 1	4				4
Bee Caves No. 2	6				6
Lake Austin Park	10	5	2		
		2	1		
			2		14
Boy Scout Hut	10	7	6		
		2	0		
			5		17
Mount Bonnell No. 1	36				36
Mount Bonnell No. 2		7	4	3	
			5	4	
				2	14
Mount Barker	11	6	4	1	
		3	1	0	
			4	2	
				4	22
Westview	21	9	7	2	
		5	2	0	
			3	1	
				4	33
Farmer's Ranch	33	21	15	7	
		9	7	3	
			12	7	
				10	64
Waters' Park	8	3			
		3			11
Lamar Boulevard	10	6	5	1	
		5	3	1	
			4	3	
				4	23
Onion Creek	11				11
					255

That is, once lost for a season, the frogs were never found again. Frogs classed as probable males comprised 59 (50.4%) of the 117 frogs that disappeared.

Assuming the movements of adults out of the area comparable to movements into the area (see below), then 27.3% of the total adult losses (59♂? and 34♀) or 25 frogs would indicate adult movements out of the area. The remaining male? and female losses (68 of 117—58.1%) would represent the minimum losses due to predation. Perhaps a possible maximum would be the total of the female and male? losses (79.5%).

Increases in the estimated population number may be attributed to 1) settlement of juveniles in the area, 2) dispersal of juveniles through the area, 3) dispersal of adults into the area. In the original markings (spring 1951) 149 frogs were observed; 29 new frogs were found in the fall of 1950, 35 in the spring of 1951, and 24 in the fall of 1951. An analysis of these data may indicate the percentage of increase attributable to each of the above factors. As the growth data indicate that a juvenile can grow to 25 millimeters in the course of the winter season and to even larger size in the summer season, all new individuals of this size or smaller are considered juveniles.

Only 15 (17.1%) of 88 of the new frogs were adult females. Nine (10.2%) of the new frogs were adult frogs classed as probable males, which, when added to the adult females, indicated that 27.3% of the new frogs were adults. On the other hand, 64 (72.7%) of the 88 new frogs were juveniles. Thus there is little doubt that juvenile individuals accounted for most of the replacement in the population. These juveniles may have been born on the plot or may have dispersed there from surrounding areas.

SEX RATIO

Estimates of the sex ratio in the cliff frog are subject to several errors. The frogs on the home-range plots are difficult to sex, because there are no reliable secondary sex characters. Frogs with eggs developed sufficiently to be seen through the abdominal wall can be definitely classified as females. There is no method for distinguishing the eggless females from the males without killing each individual. Thus some of those frogs considered males were almost certainly females.

Forty-eight of the 255 frogs marked in the home-range studies were juveniles while they were on the plot and could not be sexed. Sixty-six of the 255 frogs were found with eggs present and were known to be females. The remaining 141 frogs were classified as probable males. The chi square of this ratio indicates that the difference from the expected 50:50 is highly significant. This difference probably can be attributed to the difficulty of accurately sexing the individuals.

The samples used in the study of geographic variation would be expected to have more males than females because the call of the males attracted the attention of the collector.

In a sample of 110 frogs from the study of local variation 57 of the frogs were males and 53 were females. These frogs were collected at two localities where workers searched for the frogs by use of a light or by turning rocks rather than by tracing the calls. This ratio is not significantly different from the expected.

The sex ratios at home range localities in all probability do not represent

the true sex ratio. Rather the data represent the relative activity of the males and the females and the inability to sex correctly individuals in the marked populations. A difference in the activity of the males and females is also indicated in the home range studies and has been noted in other amphibia.

DISPERSAL

The importance of dispersal in gene flow and thus in speciation has received considerable attention in population studies. Field experiments were designed to determine the conditions and results of dispersal under the following circumstances: (1) dispersal of juveniles, (2) dispersal into areas of high population density, (3) dispersal into areas of low population density, and (4) dispersal into new habitats

DISPERSAL of JUVENILES

The most important dispersal from the standpoint of population genetics is that of the juveniles, for here is usually found most of the gene flow between populations or sub-populations.

The method used to study the dispersal of juveniles consisted of marking and releasing the juvenile frogs collected in a given area at one point, thus allowing a constant reference point and limiting to some extent the area that had to be covered in order to determine the distances, directions, and paths of dispersal. This technique had various obvious limitations and errors. The differences in habitat, edaphic conditions, moisture, physiography, and locality of hatching that might have affected dispersal patterns were perhaps altered by such artificial moving of the juveniles. The dispersal patterns were based on movement from one point in a given area, whereas, under natural conditions, movement would have proceeded from many different points.

Two localities, Mount Bonnell and Farmer's Ranch, were used for the study of juvenile dispersal. Mount Bonnell consists of a bluff and talus slope running north-south with west downhill and east uphill. To the west of Mount Bonnell lies Lake Austin, which is a complete barrier to the dispersal of the frogs, and to the east is the cedar-capped hill of Mount Barker, where perhaps the rock cover is so thin as to form a partial barrier to the dispersal of the frogs. Farmer's Ranch is a quarry, where a bluff face and scrap fragments run north-south, with east uphill and west downhill. The terraces of Dry Creek which may be a partial barrier to the dispersal of the frogs lie to the west of the quarry, and to the east occur only small and scattered rock exposures.

In May and June 1951, 53 juveniles were collected, marked and released at Mount Bonnell. Twenty-seven of these were recovered at least once. In July and August, 36 juveniles were marked at this locality, and eight of them were recovered. In September, 28 juveniles were marked of which nine were recovered. Eleven of the frogs recovered at Mount Bonnell apparently established residence.

In May and June, 51 juveniles were marked at Farmer's Ranch, and 17 of these were recovered. In July and August, 42 juveniles were marked, of which six were recovered. In September, 18 juveniles were marked and released, and ten of these were recovered at least once. Of the 33 juveniles recovered at Farmer's Ranch, six appeared to establish residence.

The 17 juveniles at both localities that had apparently established residence had dispersed from 123 to 328 yards, with a mean dispersal distance of 231±28 yards. Fifty-nine (71.5%) of the 77 frogs recovered dispersed approximately north or south along the bluffs; 22 (28.5%) dispersed at approximately right angles to the highest concentrations of rock. Twenty-four (31.2%) of the frogs dispersed to the north, 31 (40.3%) dispersed to the south, 15 (19.5%) dispersed east and uphill, and seven (9.1%) dispersed west and downhill.

Several factors (dates of the breeding season, time of hatching, abundance of moisture) may be responsible for inducing the juveniles to disperse. Juveniles have been found in all months of the year except January and December. These were the months that had the least precipitation and the lowest temperatures during the study. The juveniles were found in high numbers in April-May and September of 1950 and in May-June and September of 1951. Additional high numbers of juveniles were found on July 13, 14, 15, 1950, following 0.66 inch of rain; on August 18, 19, 1950, following 0.46 inch of rain, and on August 19, 20, 21, 1951, following 2.07 inches of rain. These frogs may or may not have been dispersing.

The distances and directions of dispersal seem to be influenced by the physiographic conditions. The dates of the breeding season, the time of hatching, and the presence of adequate moisture appear to be the conditions that affect the time of dispersal in the juveniles.

DISPERSAL INTO AN AREA OF LOW POPULATION DENSITY

The movement of frogs into an area of low population density was studied at Mount Bonnell in the spring of 1951. This was done in two phases. First the frogs in the area surrounding a segment of a bluff were marked and released. When, through the use of the Lincoln Index, an estimate of the number of frogs in the surrounding area was available, the percentage of marked frogs on this surrounding plot was calculated. Frogs were then removed from the bluff, and the movement of the marked frogs into this area of induced low population density was estimated. It was hoped that this procedure would allow an estimate of the amount and rate of movement into areas of low population density.

Six hundred yards of bluff and talus, 100 feet wide were staked out. Two fifty-foot wide parallel transects, each 700 yards long, were measured and staked. One of the transects was 150 feet to the east, and the other was 150 feet to the west of the bluff. Fifty-foot wide plots were staked out to connect the ends of the two transects, thus completely surrounding the 600 yard segment of the bluff. Adding one-half the average home range to each edge to allow for frogs which only partially range on the plot, the surrounding area in which the frogs were marked was approximately 14.52 acres. Twenty-six frogs were marked on this outer plot in the three-night interval of May 14 to 16. Eighteen recoveries were made, and 11 new frogs were marked on May 21 to 23. Of the 37 frogs marked, four were at the north end, two at the south, 18 at the east (downhill) and 13 to the west (uphill). The total population was estimated by the Lincoln Index as 41.88 frogs. Thus the 37 marked frogs represented 88% of the population on the outer plot, and the

estimated population by segments was distributed as follows: north—4.5, south—2.4, west—14.8, and east—20.3.

From May 17 to June 15, 1951, 87 frogs were removed from the bluff. Seventeen of these were marked frogs that had moved in from the adjoining area. If we may assume that these 17 frogs represented approximately 88% of the frogs that actually dispersed into the area of lowered population density, then in a period of 30 days, 19.3 (46% of the original 42) frogs were induced to move distances of 150 to 200 feet by the removal of 87 individuals from a central area. The average home range of frogs on the Glen Rose open slope was found to be approximately 0.15 acres which is an area less than 80 feet in diameter. Thus this movement of 150 to 200 feet into the area of low population density would represent from one and one-half to two times the normal movement of the frogs. In a similar study on the wood mouse (*Peromyscus leucopus*) Stickel (1946) found that these mice moved in less than two weeks from one and one-half to three times the distance across the average home range in response to an induced low population density. Blair (1940) found that an 85 per cent removal of the resident population of these mice would result in a movement into the depopulated area for about two weeks until approximately 50 per cent of the original density is reached.

The estimated 5.7 frogs that dispersed from west moved downhill. The estimated 10.2 that moved from the east moved uphill, and seven (estimated 7.95 individuals) of these latter frogs crossed a paved road. The overall traffic on this road is not heavy, but what traffic there is usually occurs from 8 to 11 p.m. Thus these frogs moved despite exposure to car lights, and very open terrain.

Eighteen (43%) of the estimated 41.88 frogs were known to remain in the outer plot from seven to 10 days. These 18 marked frogs represent the minimum number of resident individuals in the outer 14.5 acres. In all probability a considerable portion of the remaining 24 marked individuals were residents of this outer plot. Nine (53%) of the 17 marked frogs recovered from the inner area of induced low population density were known residents of the outer plot. There is little doubt that the cliff frogs will respond to local areas of low population density by movement into the depleted habitats.

DISPERSAL FROM AN AREA OF HIGH POPULATION DENSITY

In an attempt to determine whether or not there is dispersal of cliff frogs from an area of high population pressure, 25 frogs were added to the Mount Barker population on September 9, 1951. On September 2, resident frogs numbered 16 and 19 were observed. On Sepetember 8, frogs numbered 3, 15, 16, 19, and 20 were observed. On September 9, frogs numbered 3, 19, 20, ♀21, and 22 were observed, and 25 frogs (21 possible males and four females) were added to the population. Frog number 15 was not later recovered. Frog number 19 was last observed on September 11. One of the released males was recovered on September 10. Six of the probable males were recovered on the plot on both September 10 and 11. Two of these six were again recovered on September 13 in the area. One of the six was recovered on September 25 126 yards from the point of release. One of the remaining 14 was recovered 43 yards from the point of release on September 13. Another (20 mm length) was recovered on October 23 416 yards from the point of release. The distance which this frog moved may have been aided by normal,

juvenile, dispersal tendencies. None of the four females was recovered; 12 of the 21 possible males were not recovered.

One resident frog (number 15) was not observed after the addition of the new frogs. One cliff frog (number 19, 18 mm length) disappeared three nights after the addition of the new individuals. This frog was new to the plot but had been recovered five successive observation nights. It may have dispersed because of population pressure.

None of the 25 introduced cliff frogs established residence or remained on the plot for more than a few nights. Movements of introduced individuals were observed at distances of 43, and 126, and 416 yards. It seems evident that these frogs will move from local areas of high population density.

DISPERSAL INTO NEW HABITATS

Cliff frogs were found along or around various rocky habitats on the University of Texas Campus. These habitats harbored scattered individuals under sidewalks and around foundations of the buildings and especially around rocks at the east edge of the freshman field and around the Texas Memorial Museum. No frogs were found, however, in 1948, 1949, or 1950 at two localities (Clark Field and Memorial Stadium), which appeared to be ideal habitats for the frogs. Construction work in the enlargement of Memorial Stadium during the time of the study produced additional artifical rock exposures that also appeared to be ideal habitats for the frogs. Surrounding areas (within 60 to 300 yards) supported populations of *Syrrhophus*. These rocks at Memorial Stadium were carefully checked in order to observe any invasions of frogs that might have occurred. One frog was found in the rock at the southeast end of the stadium in the spring of 1951. Two additional frogs were found in the same rocks in the fall of 1951. This suggests a possible invasion of these new areas by *Syrrhophus*.

Clark Field (the University baseball park) presented another problem. The outfield fence is largely made up of a limestone bluff four to ten feet high and approximately 400 feet long. This bluff appeared ideal for *Syrrhophus*. No frogs were found on this bluff in the first three years of the study. In order to determine the effect of introduction of the cliff frogs on this bluff, the following procedure was followed. The bluff was carefully searched on May 14, 17, 20, 21, and all apparent animal life was recorded. Fourteen black widow spiders (*Latrodectus mactans*), seven orb-web spiders, four crickets, one camel cricket, and various beetles, hemiptera, and hymenoptera were observed on the bluff. No known predators on cliff frogs were found. On the 22nd of May at 8 p.m., 25 frogs from Mount Bonnell were released in the center-field segment of the bluff. The area was searched again at 11 p.m. on the 22nd and on the 23rd, 24th, and 25th of May. On the 9th of June, 25 additional frogs were released. The bluff was observed on the nights of June 10, 11, 12, and 15. It is interesting to note that the number of black widow spiders on the bluff was reduced from 14 on the 21st of May to six on the 23rd and to two on the 24th of May. No black widows were observed on June 9, 10, 11, and 12. Three were found on the 15th of June. The frogs may have preyed on these spiders or may have destroyed their webs forcing the spiders to move. On September 8, 1951, nine black widow spiders were found on the bluff.

Nineteen of the first 25 frogs and 14 of the second 25 frogs released were recovered in the baseball park. The 33 recovered frogs dispersed as follows: 10 (33.3%) above the bluff; five (15.2%) below the bluff; and 18 (54.5%) along the bluff. The area outside the baseball park for approximately 400 yards in each direction was searched each night that the bluff was searched. None of the marked frogs was recovered in this area.

The 54.5% observed dispersal along the bluff could have three possible explanations: (1) the frogs that dispersed along the bluffs were easier to observe than those in the outfield grass below the bluff, (2) the board fence, sidewalk, streets, and streetlights above the bluff may have caused frogs moving in that direction to turn back toward the bluff, (3) there could have been more actual dispersal along the rock exposures, as was found at Mount Bonnell and at Farmer's Ranch.

None of the *Syrrhophus* established residence on the bluffs. This may have resulted from lack of food supply and lack of adequate cover, or from the spraying of the bluff with green paint each spring (as an aid to baseball batters).

HOME RANGES

The home range is the area over which an animal normally travels in its search for food, mates, and home sites (Burt, 1943). The home range should not be confused with the territory, which could be defined as the part of the home range that is defended against the invasion of other individuals of the same species. There is little doubt that most animals have a home range. The importance of the home range, from the standpoint of population structure, is that it establishes a definite locality for the animal and thus limits the available individuals with which it may mate. The limit on the amount of movement and number of available mates becomes a very important factor in the consideration of the rate of gene flow through the population.

Various methods have been used for obtaining an estimate of the size of the home range. Direct observation has been used in diurnal forms such as birds, squirrels, and lizards. Live trapping of marked individuals has been found the most satisfactory method for nocturnal small mammals. Direct nocturnal observation, aided by the use of flashlights, was used in this study. The size of the home range was calculated by connecting the extreme points of capture by straight lines. This method obviously gives a much larger home range estimate than the actual area covered by the individual in its normal daily activities, because of the tendency of the cliff frog to remain in or near rock outcrops. On the other hand it does give a minimum estimate of the surface area in which mates are available.

The area over which mates are obtainable is another factor. This area is undoubtedly the distance over which the call of the male will produce a positive influence on the movement of the females. It could be considerably larger than any of the estimated home ranges measured in the study. The call of the male usually can be heard over 100 feet, and on occasion it can be heard at 100 yards. An estimate of this area will depend on the influence of the call on the female frog. The calculated sizes of the home ranges of the females would suggest that this distance may be very little, if any, larger than the sizes of the estimated home ranges. However, it should be pointed out that the size of the home range of the females is estimated only after she

enters the experimental plot. If the calls of the males induce the females to move great distances to the plot, this movement may not be shown by the data. The problem of the sex of the individuals in the home range studies has been previously discussed.

The localities were worked both early and late in the evening. Occasionally they were worked shortly before dawn. Many data were obtained by rock turning during the daylight hours. Such rock turning may have destroyed "home sites" of the individuals and disrupted and influenced their normal activity. However, the rocks were returned to their former positions in an attempt to reduce the disturbance of the habitat. The available cover may have been increased by the loosening of the rocks from the substratum.

The localities of the home range studies were previously described. These localities were chosen for several reasons. The presence of cliff frogs and the numbers of frogs present were obvious criteria for choosing a study area. The localities were also picked to sample various physiographic conditions (cliffs, talus, open slopes, and quarries) and to sample the geologic formations known to support populations of the frogs (Glen Rose, Edwards, Austin Chalk, Buda). Limitations on the time of the worker necessitated the dropping of the more distant localities from the study. There is little doubt that the available time introduced a certain bias on the number of nights each locality was studied. Only five localities were observed during the last season (fall 1951) of the study. The proximity of these localities to each other and the ease with which they could be reached were factors in the choice of these five localities for continued study. The study of three localities at one time would be the suggested limit for future workers. This number is possible only because the method of direct observation does not require such constant attention as do the trapping techniques used in the study of small-mammal populations.

The size of the average home range, the size of the plot, and the number of average home ranges are listed in table 2. The mean sizes of the home ranges were much smaller than those found in small mammals (0.51 to 0.63 acres in *Peromyscus maniculatus bairdi* (Blair, 1940); 1.97 to 10.66 acres in *Peromyscus polionotus leucocephalus* (Blair, 1951a); 0.066 to 0.154 acres in the cliff frog). Variation in the observed sizes of the home range may result from several factors: (1) the number of captures, (2) the sex of the individual, (3) season of the study, (4) ecology of the locality.

NUMBER OF CAPTURES

Blair (1942, 1951a) and Haugen (1942) suggested that a minimum of 10 observations is necessary to establish an adequate home-range size for rodents. The results of this work suggest that considerably less than 10 observations would be necessary to obtain an adequate home-range size for these frogs. There are several conditions in this study that are unlike those of small mammal populations. The movements of the frogs are typically along the rock outcrops. If the home range is based on two observations on each of two adjacent outcrops, the estimated size of the home range would tend to be increased proportionally very little by the addition of further observations on either of the same outcrops. Further, observations on isolated rocks lying between the two outcrops seldom add to the estimated size of the home range. The movements of the frogs where major cliffs

(4 to 6 feet high) were available was typically between this cliff and smaller nearby outcrops or clumps of rock. If only the cliff was observed in these areas, one would eventually find most or all of the frogs in the area. However, it was necessary to search carefully all nearby areas in order to obtain maximum movements of the frogs. It was apparent that the movements of the frogs were intensified during the peak of the breeding season. Most of the localities were studied only during the breeding season.

HOME RANGE SIZES IN MALES AND FEMALES

There was no significant differences in the mean sizes of the home ranges of the males and the females. The home range size of the females appears to be smaller than that of the males. This was probably the result of the shorter length of activity of the females, fewer observations, and the impossibility of adequately sexing the individuals.

SEASONAL VARIATION IN HOME RANGE SIZE

Observations on these frogs have demonstrated two distinct peaks of activity. For this reason the home range data were centered around a spring and fall home range. There was no significant difference between the size of the home range of the possible males or the females in the spring and fall. However, the home ranges tended to be smaller in the fall than in the spring. This was probably caused by the shorter periods of more favorable climatic conditions in the fall than in the spring.

There was considerable difference in the relative movement of individuals between summer or winter and spring or fall. In cold but wet weather in the winter individuals were typically found in one small crack in a bluff on six or seven consecutive nights. Intensive work was not done during midsummer and winter. The home ranges at these times are not extremely important to gene flow as very little if any breeding activity occurs. However, the estimated home ranges of these frogs during adverse climatic conditions were in many cases from six to 36 square feet (.000138 to .000805 acre). This estimate was based on as many as 12 observations on a single frog in a three week period.

ECOLOGICAL VARIATION IN SIZE OF HOME RANGE

An additional factor which might have affected the size of the home range was the type of geologic formation on which the frogs were studied. There is more variation between the several Glen Rose localities than between the different geologic formations. A consideration of the physiographic descriptions of the localities suggests that this variation in the size of the home range is the result of differences in the physiography rather than the geology of the localities. The variation in home-range size of possible males on four types of physiographic features (open slope, quarry, cliffs, and talus) were studied (table 5). The mean home range size of the cliff frog on the open slope is larger than those on the cliffs at approximately the five per cent level of significance. The mean size of the home ranges at the quarry is larger than that of the home ranges on the cliffs at approximately the one per cent level of significance. The mean size of the home ranges on the talus slope is significantly lower than the home ranges on cliffs, quarry, or open slope.

TABLE 5.—Size of home range of possible males during the breeding season. Six or more observations each.

Physiography	Number of Individuals	Average Number of Observations	Size of Home Range in Acres
Open slope	18	7.05	0.139 ± .014
Quarry	46	9.78	0.116 ± .007
Cliffs	81	9.53	0.081 ± .006
Talus	12	6.42	0.052 ± .006

PERMANENCE OF THE HOME RANGE

The data indicate that once the cliff frog establishes residence, the individual remains in the area throughout its life. However, it has been demonstrated that the individual will move his home range in response to local areas of low population density. Many of the individuals not only remained in the study area but utilized the same portions (groups of rocks, cracks in the cliff) of the area for over two years. Individuals appeared to have favorite sites from which they would call. There was a tendency for individuals to move from site to site during the breeding season.

The males and females apparently have comparable home range sizes. The home range sizes appear to be larger during the breeding seasons (spring and fall and smaller during the periods of less favorable conditions (winter and summer.) The trend in home range size approximates the trend in the amount of rock surface and cover available, the sizes being larger on the open slope and smaller on the talus. The permanence of the home range and their small sizes will tend to reduce the rate of gene flow in the populations.

POPULATION STRUCTURE

The importance of the genetic structure of natural populations, rate of gene flow, genetic shift, size of populations, population density, and amount and rate of dispersal have been emphasized in recent papers by Wright (1940, a, b, 1943, 1946, 1948, 1949). The variations in pattern of distribution, in population density, in concentration of individuals, in size of home range, and in rate and amount of dispersal as presented in the preceding chapters give some indication of the factors that may produce gene flow between populations and consequently may cause differentiation within and between local populations.

The distribution of the cliff frog follows the outcrop of certain geological formations (Glen Rose, Edwards, Buda, and Austin Chalk in South Central Texas). The frogs apparently are absent or occur only as scattered individuals on certain other formations (sands, clays, shales, and marls) in South Central Texas (Navarro, Taylor, Eagleford, Del Rio, Georgetown, Comanche Peak, Walnut, and Travis Peak). The formations that are occupied by the cliff frog in this portion of its range are massive limestones.

Milstead, Mecham, and McClintock (1950) found the cliff frog on the Stockton Plateau in the narrow canyons and canyon heads where there was a large amount of limestone rock coverage. Gaige (1931) found the cliff frog under the igneous and the huge boulders of the creek bed in the Chisos

Mountains of West Texas. Schmidt and Smith (1944) reported the species from rocky areas in the Big Bend National Park, and Jameson and Flury (1949) reported the frog from a few calls in the igneous Roughland Life Belt but not in the Plains Life Belt of the Sierra Vieja Mountains.

The distribution pattern of the cliff frog is mosaic in the sense that certain variations in the population densities follow variations in the physiographic conditions (open slope, quarry, talus) of the rock outcrops. The distribution is in part linear in that it generally follows along the rock outcrops. In Central Texas where the high flat plains of the Edwards Plateau are heavily dissected and the rock exposures follow the rivers and streams, the distribution pattern of the cliff frog may be referred to as dendritic (Blair, 1951 b). Wright (1943) suggested that linear distribution of a species is more favorable to differentiation resulting from isolation by distance than is an areally continuous distribution.

The effect of variations in population densities on the rate of gene flow and the amount of differentiation is closely related to the amount of dispersal into the population. If dispersal into two populations is equal, high population densities favor adaptive differentiation, and low population densities favor non-adaptive differentiation (Wright, 1943). The populations of the cliff frog are apparently small in density and in size. Thus non-adaptive differentiation or random shift ("Sewall Wright Effect") might be expected to play an important role in any geographic variation found in local populations.

Dispersal of a given number of individuals into populations of low population density and small size is proportionally higher than dispersal of an equal number into populations of high density and large size. Where population densities are low and population sizes small, as in the cliff frogs, low dispersal numbers will tend to favor both adaptive and non-adaptive differentiation. If the amount of dispersal varies to the same degree and at the same times as the variations (seasonal, year to year, etc.) in the population densities, non-adaptive differentiation might occur when dispersal rates and population densities are low, generally only adaptive differentiation will tend to be favored when dispersal rates and population densities are high.

Several factors affect the degree of random mating of individuals in a population. In types of salientians whose individuals are concentrated in breeding swarms, as in aquatic frogs, there is perhaps a greater opportunity for random mating than in types whose concentrations are low, as in terrestrially distributed forms in which the activity of the individuals is restricted to a home range. The home range studies indicate that the highest concentrations of the cliff frogs occur on and around the highest concentrations of rocks during the breeding season, which may enhance the opportunity for random mating within the local population.

Limited size of the home range will further tend to limit the number of available mates. The activity of the individual cliff frogs within the home range perhaps plays a role in increasing the number of available mates. The rate of movement of the males is highest during the breeding season. Thus the male covers a larger area in the short period of the breeding season. The influence of the call of the male in positively attracting the females may perhaps extend considerably beyond the normal home range of the male,

which would increase the area in which mates are available. This is different from small mammals such as rodents, lizards, and salamanders, which have no calls. The effect of the call of the males on the females may have some sexual selective value in that the louder or more characteristic call of a given male may enable him to better attract females.

Wright (1946) has pointed out that when the effective breeding populations are small (approximately 20 individuals) there will be considerable differentiation among local populations. He further pointed out that the amount of differentiation will be greater when each individual in the population is the result of a separate random mating (as in many vertebrates and in the cliff frogs) than when individuals are the results of matings of permanent pairs (in some mammals and birds) and considerably greater than when individuals are the result of hermaphrodites. Wright does not discuss the amount of differentiation expected in populations in which the species form breeding swarms as in most salientians and many salamanders. It would be of interest to have some knowledge of what differences would be expected in the amount of differentiation between species that form breeding swarms and terrestrially distributed species in which random mating is perhaps more restricted.

There is little doubt that the amount of differentiation in a population would be expected to be fairly large when the population is subdivided into various local populations of varying but usually small sizes and separated by varying degrees of isolation. Under these conditions there is a greater likelihood that evolution will continue in the absence of secular environmental changes. The ability to adapt to any environmental changes is much greater when the population is subdivided into various local populations than when the population is homogenous (Wright, 1949, p. 474).

"Finally in a large population, divided and subdivided in partially isolated local races of small size, there is a continually shifting differentiation among the latter, intensified by local differences in selection, but occurring under uniform and static conditions, which inevitably brings about an indefinitely continuing, irreversible, adaptive, and much more rapid evolution of the species than in a comparably large, random breeding population." (Wright, 1948, p. 280.)

The pattern of distribution and population structure of the cliff frog apparently fits rather closely the conditions (small population size and density, each partially isolated) that tend to favor differentiation.

MORPHOLOGICAL VARIATION

DIFFERENTIATION OF LOCAL POPULATIONS

The mosaic, linear, and dendritic distribution pattern, the small sizes and densities of the cliff frog populations, and the partial isolation of the various sub-populations on several geologic outcrops would be expected to favor differentiation of the various local populations. In order to determine whether or not any variation exists between these local populations, samples were collected from 12 localities in Williamson, Hays, and Travis Counties, Texas (table 6).

Seven measurements were made on each specimen for comparison of the different sub-populations. Measurements of the snout-vent length, width of the head, length of the hand, length of the foot, length of the forearm, and length of the shank were made on each individual with a vernier caliper. The

variation in the amount of pigment in the dorsal pattern was measured by use of a Whipple micrometer disc which had a grid of 100 squares (10 on each side). By use of a 10X eyepiece and a 1.3X objective, each square was approximately 0.5 mm on a side. The grid was placed in the mid-dorsal line immediately posterior to the eyes, and the number of squares with 50 per cent or more dark pigment was counted. In order to adjust for individual variations in size, the width of the head, length of the hand, forearm, foot, and shank, and the number of squares with 50 per cent or more pigment were divided by the snout-vent length of the individual. The angle of the snout of each individual was determined by comparison of the snout with various angles of known dimensions, which ranged from 40 to 100 degrees at five degree intervals. This measurement did not vary with the size of the individual, and the data concerning these angles are presented in absolute terms rather than as a proportion of the snout-vent length. It is assumed that any differences produced by the variation in preserving technique would affect all measurements equally and thus would not result in deviations in the proportions. Individuals of less than 20 mm snout-vent length were excluded from the calculations as immature. There was no statistical difference between the males and females in any of the proportional measurements; thus the males and females were not treated separately.

In all, 456 frogs from East Central Texas (Travis, Hays, Williamson, Burnet, and Bell Counties) were measured. The number of individuals in each of the 12 samples is indicated in table 6.

The variation of the proportional measurements of the samples from the various sub-populations is considered from two standpoints: (1) variations between sub-populations (table 7) and (2) deviation of each sub-population from the regional population average (fig. 1).

The means of two populations being compared are considered to differ significantly when there is no overlap of two times the standard error of the

TABLE 6.—The locality, specimen number, and letter designation of the local populations studied. The letter designations correspond to those used in tables 7 and 9 and fig. 2.

Letter	Population	Locality	Specimen Number
A	Mount Bonnell	3 mi. N.N.W. Capitol, Austin	84
B	Balcones Cave	5 mi. N.N.W. Capitol, Austin	51
C	Waters' Park	10.4 mi. N. Capitol, Austin	30
D	Lake Austin Park	8.0 mi. N.W. Capitol, Austin	30
E	Merrell's Cave	13.0 mi. N. Capitol, Austin	29
F	Onion Quarry	7.0 mi. S.S.E. Capitol, Austin	37
G	Onion Creek	14.0 mi. S.S.W. Capitol, Austin	26
H	Boy Scout Hut	2.0 mi. W. Capitol, Austin	33
I	Gaines Ranch	4.8 mi. W.S.W. Capitol, Austin	55
J	Oak Hill	8.0 mi. W.S.W. Capitol, Austin	29
K	Steam Cave	5 mi. S.W. Georgetown	17
L	Ezelles Cave	1 mi. S.W. San Marcos	18

TABLE 7.—Percent level of significance of differences (indicated at the one and five percent levels). Letter designations of localities are given in table 6. Character designations are given in table 8. Distance in miles between localities is given in each case.

		A	B	C	D	E	F	G	H	I	J	K	L
								1%					
A			2,S	6	5,SFW	11	12,SL	17	4	6,SA	10	25,SF	30,SAH
B		2		4,S	4	9	12,D	18	5	8,DWL	11	23,FL	33,H
C		6,L	4		7,F	5	16,D	22	9	12,DSL	14	20,SFL	36,SAH
D		5,A	4	7,S		10	15,DL	18	7	8,DW	9	23	32
E		11	9	5	10,S		20,DL	27	14	16,D	18	15	45,SAH
F		12,AW	12	16,S	15	20		11,L	8,L	8,WL	11,DL	36,DL	25,HL
G	5%	17,AW	18	22	18,S	27	11		13	10,HW	10	42	15,S
H		4,SWL	5	9	7	14	8	13		3,WL	6	28,L	29,S
I		6	8	12	8,H	16,W	8	10	3,H		3	31,F	28,S
J		10	11	14	9,S	18	11	10	6	3,DH		33,F	24,SH
K		25	23	20	23	15,S	36	42,SL	28	31,D	33,S		55,H
L		30	33	36	32	45	25	15	29	28	24	55	

mean of each population. The *t* test of Fisher (1946) and Snedecor (1946) was used to express the percentage level of probability that the two populations were different. The percentage level of probability of difference between the several populations is summarized in table 7.

If each of the 12 populations was significantly different from every other population in all of the seven characters, there would be 462 differences. There were 65 (14.1%) highly significant and differences and 24 (5.2%) significant differences for a total of 89 (19.3%) differences out of the possible 462 (table 7). Using the same method of computing the percentage of differences, Flury (1951) found 32.5% and 34.4% differences betweeen populations of the tree frog (*Hyla versicolor*) from East Texas and Central Texas, respectively. It may be that the tree frog has a pattern of distribution in smaller or more isolated populations and has lower rates of dispersal than the

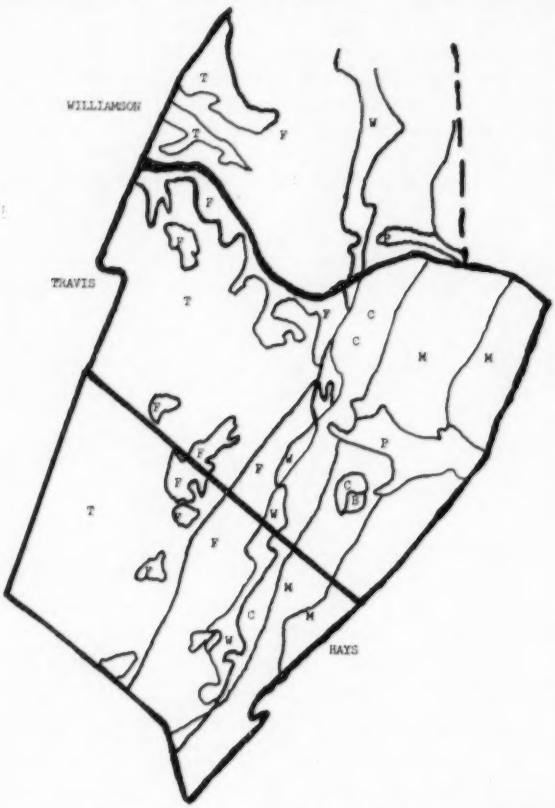

FIG. 1.—General distribution of the major geologic formations in Williamson, Travis, and Hays Counties, Texas. *Cretaceous*.—GULF SERIES: Montana (M), Colorado (C); COMMANCHE SERIES: Washita (W); Fredericksburg (F), Trinity (T); IGNEOUS BASALT (B). *Pleistocene River Terrace* (P). From: Dept. of the Interior, U. S. Geological Survey, Geologic Map of Texas.

cliff frog. The tendency of the cliff frogs to move rather rapidly when in unfavorable situations may indicate the ability to cross some apparent barriers, which should result in considerable gene flow between sub-populations. This gene flow could result in the swamping of some of the random shifts that might occur as result of small population sizes and densities.

If one population was different from the 11 other populations in all seven of the characters studied, there would be 77 differences. Using these 77 differences as a crude index, the variability of the 12 populations is listed in decreasing order as follows: Gaines Ranch, 25 (32.4%) differences (19 at 1% level of probability, 6 at 5% level of probability); Onion Quarry, 22 (28.6%) differences (18 at 1%, 3 at 5%); Mount Bonnell, 22 (28.6%) differences (13 at 1%, 9 at 5%); Ezelles Cave, 18 (23.4%) differences (18 at 1%); Steam Cave, 18 (23.4%) differences (13 at 1%, 5 at 5%); Onion Creek, 18 (23.4%) differences (13 at 1%, 5 at 5%); Water's Park, 15 (19.5%) differences (12 at 1%, 3 at 5%); Lake Austin Park, 14 (18.2%) differences (8 at 1%, 6 at 5%); Balcones Cave, 9 (11.7%) differences (9 at 1%); Oak Hill, 9 (11.7%) differences, (5 at 1%, 4 at 5%); Boy Scout Hut, 9 (11.7%) differences (5 at 1%, 4 at 5%); Merrell's Cave, 8 (10.4%) differences (6 at 1%, 2 at 5%). Gaines Ranch showed a variability of more than 30 per cent. Onion Quarry, Mount Bonnell, Ezelles Cave, Steam Cave, and Onion Creek showed a variability of more than 20 per cent. Water's Park, Lake Austin Park, Balcones Cave, and Oak Hill showed a variability of more than ten per cent. Boy Scout Hut and Merrell's Cave showed a variability of less than ten per cent.

If each of the 12 populations was significantly different from every other population, there would be 66 differences for each character. The variability

TABLE 8.—Viability of characters. Number of differences, of 66 possible, for each character. Designations are given in tables 7 and 9 and in fig. 2.

Designation	Character	Number and Percent of Probability Levels of 1% No.	1% Percent	5% No.	5% Percent	Total No.	Total Percent
S	Shank length / Snout-vent length	15	22.7	9	13.6	24	36.4
F	Foot length / Snout-vent length	7	10.6	0	0.0	7	10.6
A	Forearm length / Snout-vent length	4	6.1	3	4.5	7	10.6
H	Hand length / Snout-vent length	8	12.1	3	4.5	11	16.7
L	Head width / Snout-vent length	15	22.7	3	4.5	18	27.3
D	Dorsal pigment / Snout-vent length	6	9.1	4	6.1	10	15.2
W	Angle of Snout	10	15.2	2	3.0	12	18.2

of the seven characters used in this study is shown in table 8. The characters that varied least from population to population were the foot length and forearm length, for only seven (10.6%) of the possible differences occurred. The most variable characters were the shank length and the head width, for these showed 24 (36.4%) and 18 (27.3%), respectively, of the 66 possible differences.

The use of radial indicators to summarize the variation of any sub-

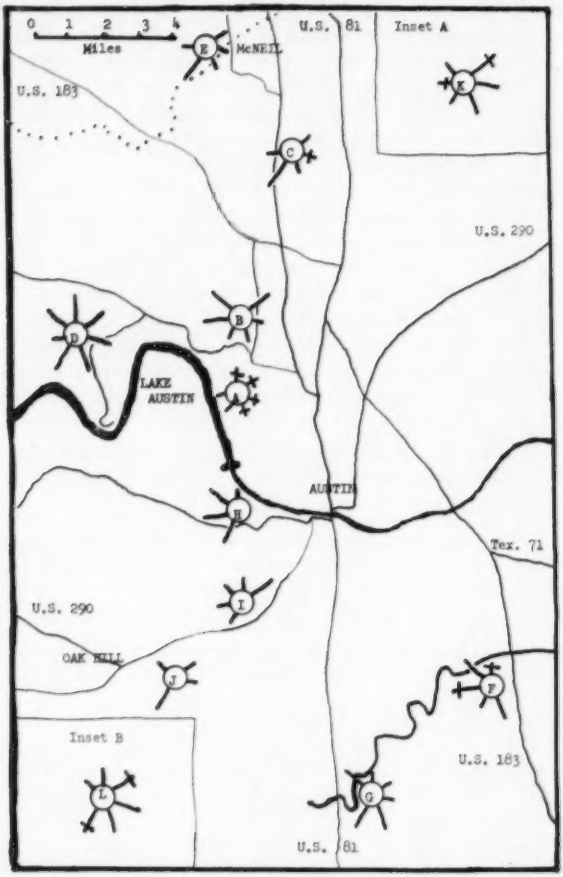

FIG. 2.—Distribution of the means of seven morphological variations in *Syrrhophus marnocki*. Each of twelve localities (table 6) is represented by a seven radiate circular figure. Radiates each refer to a particular measurement as follows: 2 o'clock radiate, shank length; 4 o'clock, foot length; 5 o'clock, forearm length; 7 o'clock, hand length; 8 o'clock, angle of the snout; 10 o'clock, width of the head; 12 o'clock, dorsal pigment (table 8). If the radiate is long, the mean of that population sample for that character lies above two times the standard error of the mean of all frogs; if short, below; if missing, within. If either the long or the short radiate is crossed, two times the standard error of the mean of the sample does not overlap two times the standard error of the mean of the whole population (See text).

population from the population average (fig. 2) has been adapted from Anderson (1949) and Carson and Stalker (1947). Each population is represented by a circle. Each of the seven radiates from the circle represent one of the characters studied. If the radiate is missing from a given diagram, the mean of that population lies within two times the standard error of the entire population. If the radiate is long, it indicates that the mean of the sub-population lies above two times the standard error of the whole population, and if the radiate is short, the mean of the population lies below two times the standard error of the overall population. If the radiate is crossed, two times the standard error of the mean of this population for this measurement does not overlap two times the standard error of the mean of the whole population for this measurement. The uncrossed radiates may indicate possible trends, while the crossed radiates represent highly significant differences of the sub-populations from the population as a whole.

Seven characters were studied in each of the 12 populations. If each sub-population differed from the entire population in each character, there would be 84 differences. The mean of a character lies within two times the standard error of the mean of all frogs in only 17 (20.2%) of the possible cases. In 54 (64.3%) of the cases, the mean of a character lies outside two times the standard error of the mean of the overall population. Significant deviation of the mean of the sub-population from the mean of all frogs was found in 13 cases. Four of these cases were in the Mount Bonnell population, one in Waters' Park, two in the Onion Quary, two in the Gaines Ranch, two in the Steam Cave, and two in the Ezelles cave population. Onion Quarry and Waters' Park are outlying localities along streams well to the east of the major distribution of the cliff frog. Steam cave and Ezelles cave are the most distant of the localities studied, the first being thirty miles north, the second thirty miles south of Austin. Mount Bonnell and Gaines Ranch are in the midst of the major population distribution in Travis County.

The tendency for a considerable deviation of the means of the sub-populations from the overall population means and from the means of the other sub-populations at distances of from two to 60 miles is indicated by the above data. It is felt that this variability is the result of differentiation, posssibly non-adaptive, of the small partially isolated sub-populations of the cliff frog.

GEOGRAPHIC VARIATION

In addition to the 456 cliff frogs from Travis, Hays, and Williamson Counties used in the study of local variation, 26 specimen from Terrell County, 24 miles from Bexar County, 12 from Bandera County, nine from Uvalde County, and scattered specimen from Kimble, Kerr, Burnet, Bell, Travis, Hays, and Comal Counties were examined in order to determine whether or not differences exist between frogs from different portions of the range. The frogs from Travis, Hays, Burnet, Williamson, and Bell Counties were grouped together and are referred to as frogs from Central Texas. Frogs from the southern part of the Edwards Plateau (Kerr, Bandera, Bexar, Uvalde, and Val Verde Counties) are grouped together and for convenience referred to as South Texas frogs. The frogs from Terrell County are referred to as West Texas frogs. Eight specimens of the related *Syrrhophus* campi Stejneger from Cameron County were examined for comparison. Specimens of the

TABLE 9.—Percent level of significance of the differences between specimens of *Syrrhophus marnocki* of Terrell County (T), Central Texas (CT), South Texas (ST), and *S. campi* (Sc) at one and at five percent levels is given. Designation of characters is given in table 8.

	T	CT	ST	Sc
		1%		
T		D S W L	D	D S F W
CT			D S W	D S F W
5%				
ST		H		D F
Sc	A	A	W	

cliff frog from Brewster County and specimens of other species of *Syrrhophus* from northern Mexico were not available at the time of this study.

The percentage level of the significance of differences betwen the means of the three segments of the *Syrrhophus marnocki* population are shown in table 9. Definite east-west clines are demonstrated in the snout angle, amount of dorsal pigment, length of foot, width of head, and length of shank. These clines are felt to be the result of gradations in selection from east to west, and well defined geographic races are not at present detectable.

Syrrhophus gaigeae (Schmidt and Smith) was described from 27 frogs from Brewster County, and the species was distinguished from *Syrrhophus marnocki* by its smaller size, wider head, vermiculate rather than spotted dorsal pattern, and the 250 miles separating the known ranges of the two species. Milstead, Mecham, and McClintock (1950) reviewed the differences between the Brewster, Terrell, and Eastern Edwards Plateau specimens and considered *Syrrhophus gaigeae* Schmidt and Smith to be a synonym for *Syrrhophus marnocki* Cope. The present study tends to support their conclusions.

The eight sepcimens of *Syrrhophus campi* are very significantly different from the Terrell County and the Central Texas cliff frogs in the amount of dorsal pigment, length of shank, length of foot, and width of head and significantly different in the length of the forearm. These eight *Syrrhophus campi* are very significantly different from the cliff frogs from the southern part of the Edwards Plateau in the length of the foot and in the amount of dorsal pigment and significantly different in the width of the head.

The taxonomic and phylogenetic status of the species of *Syrrhophus* of Northern Mexico and Texas is uncertain at present. It appears that several questions must be answered before the relationships of the various populations can be determined. The cliff frogs on the Edwards Plateau somewhat restricted to massive outcrops of calcareous limestone. The *Syrrhophus* which are found in Trans-Pecos Texas apparently occur on both calcareous and igneous rocks (Gaige, 1931; Schmidt and Smith, 1944, Jameson and Flury, 1949). No frogs were found on the scattered outcrops of igneous rocks in Travis County.

Individuals of *Syrrhophus campi* are found in the sandy river alluvium of

the lower Rio Grande Valley, and the known range extends south and west into Tamaulipas, Nuevo Leon, and San Potosi, Mexico. We have every reason to believe that the Central Texas *Syrrhophus* extend south into Mexico following the Balcones Escarpment. Somewhere in Northern Mexico, the ranges of *Syrrhophus campi* and *Syrrhophus marnocki* can be expected to be congruent. Two other species of *Syrrhophus* (*S. latodactylus* Taylor, *S. smithi* Taylor) have been described from Northern Mexico. Both *S. latodactylus* and *S. campi* occur in Nuevo Leon and San Louis Potosi. *S. smithi* is known only from the type locality (15 miles west of Galeana, Nuevo Leon, Mexico).

Extensive study of the various populations, especially in the areas where two or more of the described species occur, will be required in order to determine whether or not the various populations behave as separate species and if so what are the isolation mechanisms which maintain their separate identities.

SUMMARY

The environmental relations, home range, population structure and breeding behavior in natural populations of the cliff frog (*Syrrhophus marnocki*) were studied in South Central Texas from 1948 to 1952 in an attempt to estimate the influence of these factors on the geographic differentiation of local subpopulations.

The standard techniques of amphibian life history studies and the methods used in the study of small mammal populations were adapted to the study of this entirely terrestrial frog. A total of 255 amphibians were marked, released, and recaptured to obtain estimates of sizes and densities of the various subpopulations, changes or turnover of the individuals in the populations, sex ratio, home range, and dispersal.

The activity of the amphibian was found to be influenced by precipitation, temperature, relative humidity, light intensity, and ground moisture. The greatest activity of the cliff frog was found to occur following spring and fall rains, when temperatures ranged from 66°F to 75°F. and when relative humidity varied from 76% to 100%. Higher light and wind intensities apparently restrict the activity of the frog. Both low ground moisture and excessive moisture apparently curtail the activity of this amphibian.

The local distribution of the cliff frog is closely associated with the occurrence of certain Cretaceous limestones (Glen Rose, Edwards, Buda, Austin Chalk). These rock and cave dwelling frogs seem to occur only on those formations where outcrops of massive rock exposures are found. The frogs were found to feed principally on insects. Ants perhaps form a large portion of the food, and during the breeding season, the frog probably partakes heavily of the large populations of the camel crickets (*Ceuthophilus*). At least three mammals (*Peromyscus pectoralis, Mephitis mephitis, Dasypus novemcinctus*) are suspected to be competitors with the frog for food. Known predators on the cliff frog populations include: *Crotalus atrox, Agkistrodon contortrix,* and *Thamnophis eques.*

The breeding season of *Syrrhophus* was found to extend from February to early December with peaks of breeding activity during the spring and fall rains. The selection of a breeding site was perhaps dependent on the activity of the male frog. The males have two distinct calls, a typical cricket-

like call, which is heard throughout the year, and a rather striking call heard only during the height of the breeding season. The mating pattern is complex. The eggs are laid in a small trench dug in moist earth by the female and covered by both the male and female as the eggs are laid. The large-yolked eggs and the laying behavior suggest that the embryological development is similar to that described for *Eleutherodactylus*. The males may mate several times in one year. There is evidence that the females may mate one, two, or occasionally three times a year.

The rate of growth was found to be greater in the spring and summer months than in the fall and winter months. The rate of growth decreased as the frogs became larger. The frogs are believed to reach sexual maturity at from 18 to 22 millimeters in length.

The population densities were found to vary from 1.2 to 8.9 frogs per acre. The lowest densities were found in the open slopes (1.2-2.0 frogs per acre). The cliffs and quarry (3.5-6.4 frogs per acre) were intermediate in population density, while the talus slopes supported the highest population numbers per area (6.9-8.9 per acre). There was a general tendency for the population densities to be higher in the spring than in the fall.

The number of individuals per available home range area varied from 0.14 to 0.74 individuals, indicating that some areas of the experimental plots were devoid of any frog activity. These areas were found to be the areas which did not contain rock exposures.

The amount of turnover of the individuals in the population suggests that about three years is the limit of the survival of the individuals. The losses of individuals were apparently greater through the summer (36.4 and 38.9%) than through the winter (30.0%). The major cause of the reduction of population numbers was probably predation.

Sex ratios were found to be approximately two males: one female. The difficulty in sexing the individuals is felt to be largely responsible for this ratio. The ratio may represent some difference between the activity of the males and that of the females.

Seventeen juveniles dispersed from 123 to 328 yards (mean, 231 $\pm$ 28 yards) before establishing residence. The breeding season, time and locality of hatching, and presence of adequate moisture appeared to be principal factors controlling the dispersal of the juveniles. Most juvenile dispersal occurred along the rock exposures.

When individuals were removed from one part of an experimental plot, the frogs in the surrounding area tended to move into the area of induced low population density. The removal of 87 frogs from an eight acre transect induced the movement of from 150 to 200 feet of 19 (46%) of the 42 frogs in the surrounding 14.5 acres.

Twenty-five frogs (21 possible males, 4 females) were added to the area of a marked population in an attempt to obtain an estimate of the movement of frogs from an area of high population density. Seven of the added probable male frogs were recovered on the experimental plot. None of the added amphibians established residence. One resident frog was not observed after the addition of the 25 new frogs.

The sizes of the home ranges during the breeding season varied from 0.02 to 0.31 acre. The largest home ranges occurred on the open slopes (0.139

± .014). The mean of the home ranges at a quarry was found to be 0.116 ± 0.007, and that on cliffs was 0.81 ± 0.006. The smallest home ranges (0.052 ± 0.006) were found on talus slopes. The home ranges were smaller, but not significantly smaller, in the fall than in the spring. When rainfall was low and environmental conditions adverse during the winter and summer, the home ranges were found to be much smaller than the home ranges during the breeding season.

The mosaic, linear, and dendritic distribution pattern, the small sizes and densities of the cliff frog populations, and the partial isolation of the various sub-populations on several geologic outcrops would be expected to favor non-adaptive differentiation in the various local populations. Considerable significant deviation within and between samples from local populations was found and is believed to be the result of shifting differentiation. Selection on these local differences would be expected to result in a rapid evolution of the species.

Definite east-west trends are demonstrated in the snout angle, amount of dorsal pigment, length of foot, width of head, and length of shank. These clines are felt to be the result of gradations in selection from east to west, and well defined geographic races are not at present detectable.

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Correlation of Physiological and Behavior Indexes of Activity in the Study of Plethodon cinereus (Green) and Plethodon glutinosus (Green)[1]

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The relative activity of closely related species may be studied 1) by physiological indexes of activity and 2) by comparative behavior responses. In order to understand the ecological relationships of animals, it is necessary to use both methods. The present study attempts to correlate these approaches to the problem of animal activity.

The two species chosen for this work, *Plethodon g. glutinosus* (Green), the slimy salamander, and *P. c. cinereus* (Green), the red-backed salamander, were selected because their habitats overlapped and there should be environmental factors common to both species. *P. glutinosus* is distributed over most of the southeastern part of the United States (Bishop, 1943). Specimens have been reported as far north as New York, Ohio, and Indiana; and as far west as Texas, Missouri, Arkansas, and Louisiana. The range of the red-backed salamander is from Georgia and Arkansas in the south, to Gaspesia and Cape Breton Island in the north; from Minnesota and Fort Williams, Ontario, in the west, to the Atlantic Ocean in the east. In comparing the general distribution of these two forms, one notes that *P. cinereus* is found in more northern situations, while *P. glutinosus* is partial to southern regions, although there is a great overlapping of distributional ranges of the two species.

The habitat of *P. glutinosus* is usually beneath logs or stones in wooded ravines, although Bishop (1927) found some slimy salamanders in a shale bank of a road-cut and away from the forest. He also stated that *P. glutinosus* may be found where there is little apparent moisture but always where it has access to crevices in banks or burrows in the soil. Shelford (1913) observed that numbers of *P. glutinosus* are found in beech woods only in moist seasons, but commonly they are in ravines where the evaporation rate is lower.

P. cinereus is mainly found in wooded regions beneath decaying logs, bark, stones, etc. Although they are well adapted to terrestrial life and may be found in fairly dry situations, they occur in greatest numbers where the moisture content is maintained by trees. Bishop (1927) states that the red-backed salamander showed no preference for any kind of forest, but may be found in evergreen, mixed, or deciduous forests, whether virgin or second growth.

Although these two species usually are not found together in the mountains of North Carolina, in Indiana they are frequently recovered from under the same log or rock. At the southern limits of the range of *P. cinereus, P. glutinosus* is found in greater numbers; but in the northern limit of the range of *P. glutinosus, P. cinereus* is more abundant (Hairston, 1949; Vernberg, 1952b). Indiana, therefore, presents an area where these two forms are apparently in direct competition for the northern extension of the range of *P. gluti-*

[1] Portions of this study were completed at DePauw University and Purdue University.

nosus. A comparative study of their activity would be of value in better understanding one phase of this competition.

The physiological studies include measurements of the rate of oxygen consumption, blood sugar determinations, and measurements of red blood cell size and number; behavior studies include responses to light of different wave lengths, soil pH gradients, and soil moisture gradients.

MATERIALS AND METHODS

Light.—The reactions of *P. glutinosus* and *P. cinereus* to white light of different intensities and to various monochromatic lights were studied by means of a box divided into two compartments by a partition that extended to within six inches of the floor; this arrangement permitted the animals to pass freely from one side to the other, but did not allow the light from one compartment to interfere with that of the other. The floor of the entire box was covered uniformly with a layer of dry soil. Half of the box was covered by a small removable light-proof lid containing a light socket in which light bulbs could be inserted; this half was called side "A". The other half was open at the top and this portion was called side "B".

To establish a light gradient, one type of light bulb was placed in the small light-proof lid, which was fastened in place over side "A". A lamp was arranged in the desired position over side "B". All the experiments were conducted in a darkened constant temperature (23°C) room.

Both colored (red, blue, and green) and white light bulbs were used. The colored bulbs were General Electric bulbs, 25W. Each light was analyzed by means of a prism spectrometer. The red bulb was all red, and the wave length was from 6,500-7,500 Angstrom units. The green bulb emitted mostly green light and the wave length was from 4,500-5,500 Angstrom units. The blue bulb was not pure but contained some green and red wave lengths.

The white light bulbs were Champion light bulbs and were of two sizes, 15 and 60W. Different intensities of white light were obtained by regulating the distance from the light bulb to the floor of the box; the intensity was measured by means of a Weston Photronic Foot-Candle Meter, Model 614.

Eight gradients were studied; for each gradient, 20 tests were carried out using both *P. cinereus* and *P. glutinosus*. The animals had a choice between a light on one side of the box and darkness on the other side in the first five gradients. These light gradients were as follows: Gradient I, nine foot-candle-darkness; Gradient II, one foot-candle-darkness; Gradient III, red-darkness; Gradient IV, green-darkness; and Gradient V, blue-darkness. The three remaining gradients were: Gradient VI, one foot-candle of white light-red light; Gradient VII, one foot-candle of white light-green; and Gradient VIII, one foot-candle of white light-blue light.

In the first five gradients, the animals were placed in the lighted side of the light box; whereas, in the last three gradients, half of the time they were placed in side "A" and half of the time in side "B". Thus, the animal initially was equally exposed to both light components.

Each test lasted for 15 minutes. When a light-dark gradient was employed, the time that elapsed from the beginning of a test until the animal crossed into the darkness was called the reaction time. The total time a salamander stayed in side "A" and side "B" was totaled and recorded. Whenever the animal passed from one side to another, this was referred to as a crossover

and was noted and totaled at the end of a test. At the conclusion of the testing interval, the specimen was removed and placed in a container. Animals to be tested were kept from all light until they were introduced into a gradient. After an animal had been tested, it was not used again for at least one hour.

Soil Moisture.—The reactions of *P. cinereus* and *P. glutinosus* to different soil moistures were studied. A box twenty inches square was divided into four compartments, with a wooden platform five inches square in the center. Each compartment was filled with soil of a pH of 7.1, and varying amounts of distilled water were added to each compartment. At the beginning of each test a sample of soil was taken and the percent of water in the soil was determined by the wet weight-dry weight method. The animals were placed on the platform in the center of the box, and the top of the box was fixed in place. At the end of forty-five minutes the top was removed and the distribution of the animals was noted.

Soil pH.—The study of the reactions of *P. cinereus* and *P. glutinosus* to soil hydrogen-ion concentration was observed in the laboratory by allowing the animals to choose between two soils of different pH. A wooden box was used in which a partition one inch high separated the floor of the box into two sections, each section containing a soil of different pH.

In the first gradient studied the soil in one section had a pH of 5.8, and the other section a soil with a pH of 6.3. The second gradient had soil of pH 6.2 in one side, and soil of pH 7.2 in the other. A uniform soil moisture content was maintained in all experiments.

To determine the pH of the soils a Beckman Glass Electrode pH meter, Model G was used. The procedure for finding the pH of a soil sample at field moisture content was that used by Reed and Cummings (1945).

Twenty ten-minutes tests were performed on both species for the first soil pH gradient, and sixteen tests for the second. For half the tests the animals were placed in one section of the gradient, then the procedure was reversed for the remainder of the tests. No animals were used more than once during an hour. The number of crossovers as well as the total time an animal was in each of the parts of the soil gradient were recorded.

Field soil samples were collected in an airproof container from the habitat from which salamanders were recovered. These samples were brought to the laboratory for the pH determinations.

All soil samples were collected in Parke and Putnam counties in Indiana. Many more soil samples were collected for *Plethodon cinereus* than for *P. glutinosus*, but this merely reflected the relative abundance of these two species in this general area.

Hematology.—The blood studies consisted of the red blood cell counts and the measurement of the size of the erythrocytes. This study was made during the spring months, and the salamanders were maintained in the laboratory at room temperature. Measurements of red blood cell size were done by means of a Spencer micrometer, using blood smears stained with Wright's stain. The width and length of 500 cells were measured. This represented blood samples from five individuals of each species. Standard techniques were used in determining the number of red blood cells. In order to insure more nearly accurate results, five individual counts were made from each pipette and then the average was taken as the final count.

Blood sugar levels were determined by the standard Folin-Wu micromethod. The blood was collected directly from the heart of the animal. Preparatory to collecting the blood, the brain of the animal was crushed by forceps and the heart was exposed. Because of the small blood volume of *P. cinereus* it was necessary to use combined blood samples for the determination of their blood sugar level.

Oxygen Consumption.—The oxygen consumption of adult specimens of *P. cinereus* and *P. glutinosus* was determined during the spring months. Animals were fed when brought into the laboratory and one week later oxygen uptake was determined. With slight modification the closed manometric method described by Wilder (1937) was employed for measuring oxygen consumption in air of these forms. All tests were conducted at 20°C. Results are reported as cubic millimeters of oxygen consumed per gram (wet weight) of animal per hour.

Results and Discussion

Light.—Results show that both *P. glutinosus* and *P. cinereus* are negatively phototropic; this is in accord with the findings of others working with different species of salamanders (Bishop, 1927; Cole, 1922; Hawes, 1945; Pearse, 1910; Reese, 1906). In the first five gradients studied, where animals had to choose between light and darkness, the specimens always were found in the darkness for the greatest amount of the total tested time (fig. 1).

Pearse (1910) stated: "The rays toward the violet end of the spectrum are apparently most potent in producing photic reactions and the rays toward the opposite end approach in their effects the condition brought about by dark." For the red-backed salamander blue light was less stimulating than red or green. In contrast, the slimy salamander avoided blue light more than red or green.

The reaction time of *P. cinereus* to these various light gradients was faster than that of *P. glutinosus*, except when subjecting them to the blue-darkness gradient (fig. 2). An inverse relationship was noted when observing the reac-

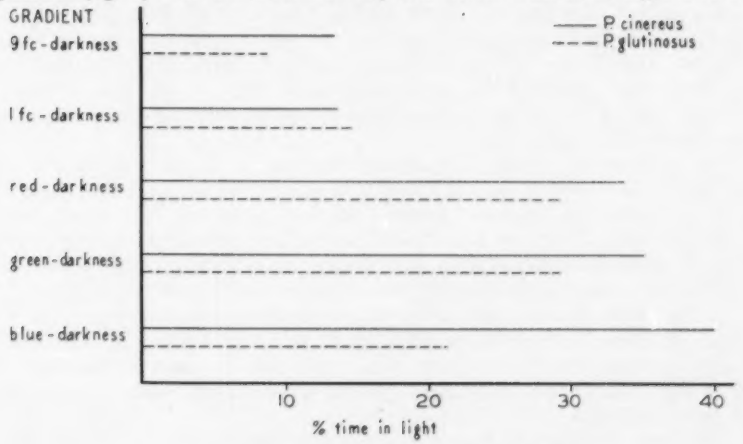

FIGURE 1. Reaction to various light gradients

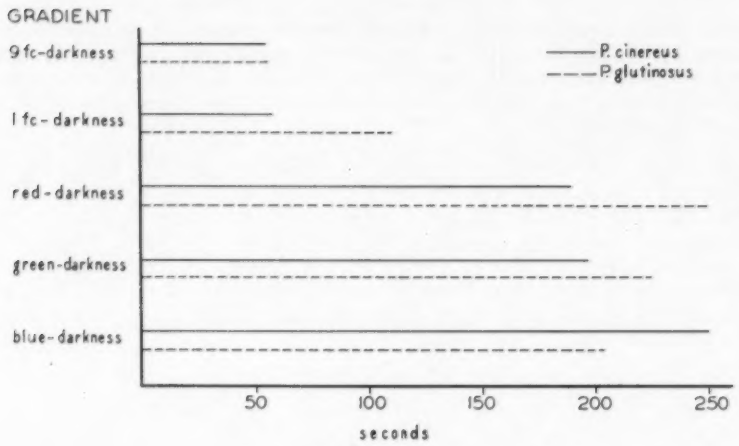

FIGURE 2. Reaction time to various light gradients

tion time of *P. cinereus* and *P. glutinosus* at the red end of the spectrum; the reaction time of *P. cinereus* is faster, but at the blue end *P. glutinosus* reacts fastest. The behavior of *P. glutinosus* to the light gradients used in this paper is typical to what one would expect from a nocturnal animal, however, the decreased sensitiveness to blue light by *P. cinereus* revealed a marked physiological difference between the two species. Perhaps this indicates that *P. cinereus* is less negatively phototropic than *P. glutinosus* and might venture forth from its burrows early in the evening when some daylight still persists. In field studies, Hairston (1949) found a trend from incomplete to complete nocturnality in the various species of *Desmognathus* studied.

It is interesting to note that Hairston (1949) found that *P. glutinosus* was active on the forest floor in greatest numbers around 11:00 P.M. and gradually diminished in the early morning hours. *P. cinereus* was observed by Park, Lockett, and Myers (1931) to become active by 8:45 P.M. but too few specimens were observed to ascribe any definite time of maximum activity. A comparative field study in a common locale should be made in order to compare these two species.

In response to a white light of nine foot-candles, the reaction time of *P. glutinosus* was twice as fast as it was to a white light of one-foot candle; *P. cinereus* showed no difference between the two intensities. This would seem to indicate that *P. cinereus* has a lower threshold for stimulation by white light than *P. glutinosus* and that when stimulated it reacts to its maximum, whereas, *P. glutinosus* reacts proportionately with increased intensity of white light.

When these animals were subjected to a gradient involving two types of lights, *P. cinereus* stayed in the white more than in the green (fig. 3). In all other experimental conditions both species preferred the monochromatic to the white light. The reason for this response is unknown but would be expected of nocturnal animals.

In these experiments, it is very significant that in each of the first five gradients, *P. cinereus* had a greater number of crossovers than *P. glutinosus*

(fig. 4). Thus, it would appear that *P. cinereus* is more active in exploring both parts of a light gradient than *P. glutinosus*. This is correlated with the findings represented in fig. 1, in that *P. cinereus* spent more time in light than did the slimy salamander and indicates that light has the least influence on the former. Added evidence for this conclusion is noted by the results of the last three gradients. When animals were exposed to a gradient of two different lights, *P. cinereus* was no more active than in the previous five gradients as shown by the number of crossovers, but the number of crossovers for *P. glutinosus* increased.

No distinct difference was noted in the reaction of the two color phases of *P. cinereus* in any of the experimental gradients used in this study.

Soil Moisture.—Table 1 summarizes the results of the responses of these forms to a soil moisture gradient. *P. glutinosus* showed a greater preference for the moist end of the gradient; whereas, *P. cinereus* was not significantly selective of either type of soil.

The importance of moisture to salamanders is well known. As mentioned earlier, Shelford (1913) and Bishop (1927) have made field observations on the influence of moisture on these two species. Shelford (1913) found in laboratory studies on the reaction of these species to a gradient of evaporating power of the air that *P. glutinosus* was more sensitive to dryness than *P. cinereus*. Rosenthal (1953) reported on the importance of soil moisture to *Aneides lugubris*. The role of soil moisture in the hibernation of *P. cinereus* was demonstrated by Vernberg (1953). However, a quantitative study on the influence of soil moisture has not been reported.

Soil pH.—The importance of soil pH on habitat preference has been of interest for some time to the ecologist. At first pH appeared to be the solution for numerous biological problems, but as the knowledge of the pedologist increased, it was shown that soil pH was closely correlated with many other variables, i.e. degree of base saturation, availability of certain chemicals in the

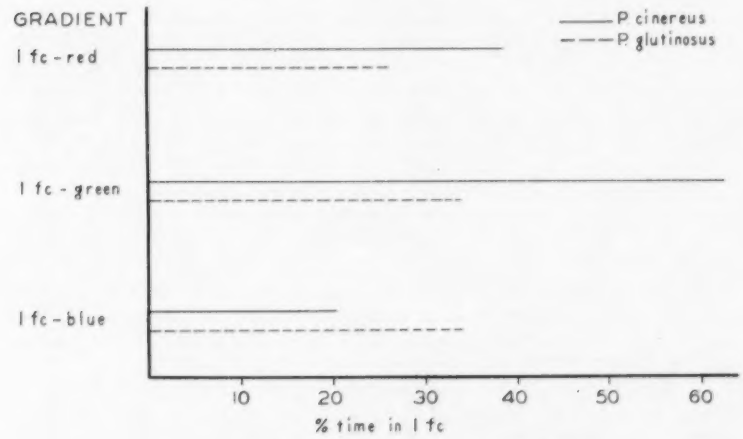

FIGURE 3 Reaction to various light gradients

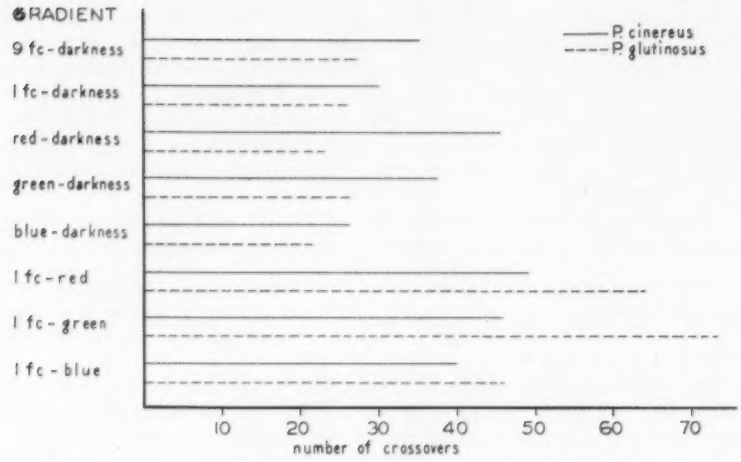

FIGURE 4. Reaction to various light gradients

soil, degree of nitrification, etc. However, soil pH is still a valuable indicator of these correlated conditions.

Some earlier studies were conducted on the influence of soil pH on a readily observable soil dwelling animal, the earthworm (Arrhenius, 1921, Phillips, 1923; and Salisbury, 1923). Allee *et al.* (1930) concluded that soil pH *per se* has very little to do with earthworm distribution.

Apparently the reaction of terrestrial salamanders to soil pH has not been reported in the literature and a comparison of laboratory findings and field observation would add information on this phase of salamander investigation.

When tested in the laboratory both kinds of salamanders had a preference for less acid soil (table 2). In the first gradient each species spent 82% of the

TABLE 1.—Reactions of *P. glutinosus* and *P. cinereus* to soil moisture content (45 minute tests)

	glutinosus	cinereus
Number of tests	22	24
Animals in soil with moisture content of 11.7 and 15.2%	4	10
Animals in soil with moisture content of 29.3 and 36.8%	18	14

TABLE 2.—Reactions of *P. glutinosus* and *P. cinereus* to *hydrogen-ion* concentration of the soil (10 minute tests)

	glutinosus	cinereus
GRADIENT 1		
Number of tests	20	20
Percent of time in pH 5.8	18	18
Percent of time in pH 6.3	82	82
Number of crossovers	21	46
GRADIENT 2		
Number of tests	16	16
Perceent of time in pH 6.2	42.5	50
Percent of time in pH 7.2	57.5	50
Number of crossovers	10	18

TABLE 3.—Number of *P. cinereus* and *P. glutinosus* found in relation to soil pH.

pH Range	Number cinereus	glutinosus
7.2-7.4	8	4
6.9-7.1	6	6
6.6-6.8	13	8
6.3-6.5	15	4
6.0-6.2	22	4
5.7-5.9	8	4
5.4-5.6	12	9
5.1-5.3	6	5
4.8-5.0	5	0
4.5-4.7	7	0
4.1-4.4	6	0
Total	108	44

time in the soil which has a pH of 6.3, while only 12% of the time was spent in the soil of pH 5.8. Of the twenty times animals were introduced into the more acid part of the gradient, only one specimen of *P. glutinosus* did not move to the less acid soil, but for the twenty times animals were introduced into the less acid soil fourteen animals did not leave this soil during the ten minute test. The red-backed salamander was more active than the slimy salamander as indicated by a comparison of the number of crossovers, *P. cinereus* crossing over 46 times to 21 times for *P. glutinosus*.

Reactions to the second gradient showed that *P. glutinosus* was in the acid soil (pH 6.2) 42.5% of the time and 57.5% in the alkaline soil (pH 7.2). The red-backed salamander was in the acid soil 50% of the time. Again the slimy salamander had a fewer number of crossovers.

Table 3 summarizes the results of the study of the relation of soil pH to distribution of these two species of salamanders. It is interesting to note that the soil in which *P. cinereus* was found had a wider pH range than *P. glutinosus*. No *P. glutinosus* were found in soil with a pH lower than 5.1. Apparently *P. glutinosus* shows no preference for any specific pH level, as individuals were equally distributed within the range of 5.1 to 7.4. In contrast, the greatest number of *P. cinereus* were found within the range of 6.0 to 6.2.

Field results differ from the laboratory findings in the response of these organisms. Both species preferred a soil with a pH of 6.3 to one of 5.8 when tested in the laboratory, although in the field *P. glutinosus* did not show this preference for the less acid soil and *P. cinereus* was found in a wide pH range.

Although differences between results of field and the laboratory studies do exist, it does not reflect on the validity of either method of study, but merely emphasizes the need for observing the reaction of animals both in the laboratory and in the field. Laboratory studies are necessary to show the preference or limits of toleration to a particular variable environmental factor; whereas, field studies show the relative importance of this one factor measured in the laboratory to the many phases of the environment in which the animal exists.

Hematology.—Red blood cell size of *P. cinereus* and *P. glutinosus* are given in table 4. When the length (L) and the width (W) of a cell are multiplied, it is possible to compare size. If the length is divided by the width, a comparison of shape is possible. The red blood cell size of *P. glutinosus* is

larger and more oval than in *P. cinereus*. In keeping with the theory of Smith (1925) that an inverse correlation exists between cell size and activity in Amphibia, the results of the present study would indicate that *P. cinereus* is the more active species.

In comparing results of red blood cell size of *P. cinereus* obtained with those of Jordan (1938), a slight difference is noted. He reported the cell size as 32.0 x 13.0 micra; however, the same figures for the present study are 30.7 x 16.3 micra. This slight variance might be due to any number of factors, such as the condition of the animal, geographical species differences, or seasonal differences.

An inverse relationship exists in comparing number and size of red blood cells. *P. cinereus* has the smaller sized cell but a greater number of cells (table 5).

The results of the blood sugar determination of these two species of salamanders are given in table 6. The high and the low values are included as well as the average. A correlation between blood sugar level and activity and habits of some groups of animals has been noted by certain workers (Gray and Hall, 1930; Kiermeir, 1939). This correlation appears to apply to salamanders also and indicates that *P. cinereus* is the more active species.

It seems apparent by the use of these various physiological characteristics of an active animal that on the basis of hematological data that *P. cinereus* is a more active species than *P. glutinosus*.

Oxygen Consumption.—The data obtained on the oxygen consumption of these two species of salamanders are given in table 7. When comparing meta-

TABLE 4.—Red blood cell size of two closely related species of salamanders.

Species	Length in micra	Width in micra	L x W	L/W
P. cinereus	30.688 ± 0.138	16.345 ± 0.084	501.60	1.878
P. glutinosus	33.440 ± 0.199	20.195 ± 0.103	675.32	1.656

TABLE 5.—Number of red blood cells of two closely related species of salamanders.

Species	Number of determinations	Number of cells per mm^3		
		Low	High	Average
P. cinereus	10	24,276	177,600	91,078
P. glutinosus	9	30,355	99,355	55,700

TABLE 6.—The blood sugar level of two closely related species of salamanders.

Species	Number of determinations	Blood sugar level in mg%		
		Low	High	Average
P. cinereus	10	50.8	68.4	59.1
P. glutinosus	10	35.6	55.2	48.6

TABLE 7.—Oxygen consumption of two closely related species of salamanders.

Species	Average time in hours	Number of tests	Number of individuals	Average weight in grams	Oxygen consumption (mm^3/hour/gm)
P. cinereus	12.8	24	24	0.89	50.63 ± 0.62
P. glutinosus	12.9	25	20	5.01	33.35 ± 0.84

bolic rates, a distinctly higher Qo_2 was noted for *P. cinereus* than *P. glutinosus*. In general it has been found that when comparing closely related species, animals considered to be the most active have a higher "basal" metabolic rate (Smith, 1925; Evans, 1939; and Vernberg, 1952a). Many factors, such as temperature, nutritional state, season and body size influence the oxygen consumption of animals and must be kept in mind when comparing species. All variables, except body size, were kept as constant and uniform as possible in this study. It is well-known and generally accepted that smaller organisms consume oxygen at a faster rate per unit weight and time than a larger sized animal. A distinct size difference exists between the two species used in the present study. *P. glutinosus* averaged 5.01 gms., while *P. cinereus* averaged 0.89 gms. However, even when comparing similar sized animals, *P. cinereus* had higher Qo_2 values.

A positive correlation between comparative behavior and physiological indices of activity is indicated. *P. cinereus* is more active than *P. glutinosus*. This species difference in activity would influence greatly the ecological relationships of these two species.

Both species may be found in similar habitats in the north central region of Indiana and appear to be in direct competition, whereas, in the mountains of North Carolina, they are found at different elevations. Although species competition is an extremely difficult problem to analyze because of the multiplicity of physical and biotic factors operative, it is conceivable that a more active species would have a decided advantage if other factors are kept constant.

Working with different species occupying similar ecological habitats, Lack (1945) found that birds differed in food selection and nesting sites. The food habits of *P. glutinosus* and *P. cinereus* have been studied (Hamilton, 1932; Jameson, 1944; Blanchard, 1928) and a significant difference in food preference doesn't seem to be indicated. Little is known of the breeding habits of *P. glutinosus* and a comparison of species cannot be made.

Any advantage of increased activity that one species might derive in competition with another species would influence the attempt of these organisms to extend their geographic range. The area in which this study was conducted represents the northernmost extension of *P. glutinosus*. A drastic decrease in habitats for these animals due to lumbering and grazing has increased the competition of these two species. The red-backed salamander, which could be found in a wider range of habitats than *P. glutinosus*, because of being less restricted by moisture requirements, now would have to invade areas that were occupied by the slimy salamander. Although extensive mixed population and long term distributional studies need to be made before the role of activity can be properly evaluated, some evidence exists to show that *P. cinereus* is more abundant than *P. glutinosus* in this area and thus more successful (Reynolds and Black, 1936; Vernberg, 1952a). A similar phenomenon was observed in snakes by Davis (1932), who concluded that the more aggressive *Thamnophis radix* influenced the distribution of *T. butleri*.

SUMMARY

A positive relationship between activity and results of physiological and behavior studies is found. *Plethodon cinereus* is a more active species than *P. glutinosus*.

Oxygen consumption of *P. cinereus* is higher per unit weight and time than

that of *P. glutinosus*. Hematological findings are that *P. cinereus* has smaller, but more numerous red blood cells and a higher blood sugar level than *P. glutinosus*.

Comparative behavior responses to physical environmental factors were studied. Both species are photonegative. *P. cinereus* is the most active species as determined by reaction time and total numbers of crossovers. *P. cinereus* is less sensitive to blue light than to red and green light. Reactions to soil pH gradients in laboratory show that both species prefer a soil pH range of 6.2 to 7.2. In the experiments *P. cinereus* had a greater number of crossovers. Field studies revealed that *P. cinereus* was found in a range of soil pH from 4.1 to 7.4, most specimens preferring a pH of 6.0 to 6.8. *P. glutinosus* was equally found in soil ranging from 5.1 to 6.4. *P. glutinosus* preferred soil with a higher soil moisture content than *P. cinereus*.

The possible significance of activity to the ecological relations and geographic distribution of these two closely related species of salamander is discussed.

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Anatomy of Biomphalaria Boissyi as Related to Its Infection with Schistosoma Mansoni[1]

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Among the fresh-water mollusks, planorbid snails play a significant role in the life histories of digenetic trematodes of man and livestock. Investigations of their morphology are of considerable value to both the malacologist and the parasitologist. Wright (1952) emphasized the need for studies of internal anatomy as an aid in the identification of snail vectors of bilharziasis. Although Baker (1945) presented a most comprehensive account of planorbids, the scope of his work was so broad that phases of studies pertaining to some genera and species, such as *Biomphalaria boissyi*, were not taken into account. *Biomphalaria* was considered only in a very abbreviated way and, because of a lack of specimens, no morphological details were included. Somewhat earlier, Connolly (1925) in his discussion of the non-marine mollusca of Portuguese East Africa referred to the anatomy of *Planorbis pfeifferi*, which he later (1938) regarded as *Biomphalaria pfeifferi*.

The purpose of this paper is to consider the anatomy of the planorbid snail, *Biomphalaria boissyi*, the intermediate host of *Schistosoma mansoni* and other trematodes in Egypt, the Sudan, and other African countries. This study also illustrates the general organization of a planorbid snail. One objective is to provide the malacologist and the parasitologist with descriptive morphological information and as many anatomical illustrations as possible. Emphasis is placed on the position of the internal organs and their relation to one another. Particular stress is placed on anatomical information in relation to infection of *B. boissyi* with *S. mansoni*, and its bearing on snail-parasite relations in general. Similar investigations were carried out by Faust and Hoffman (1934) in their studies of schistosomiasis in Puerto Rico.

The systematics of the genus *Biomphalaria* was considered recently in an extensive study by Amberson and Schwarz (1953). They stated that the snail intermediate host of *S. mansoni* in Africa is *Biomphalaria alexandrina*. Two subspecies were recognized: *B. a. alexandrina* Ehrenberg, with a northern distribution and *B. a. pfeifferi* Krauss with a southern distribution. However, their conclusions were based on shell characters and biological factors; they contributed no anatomical data. It is becoming increasingly evident that only after the anatomical details have been clarified that one could appreciate whether *Biomphalaria boissyi* (Potiez et Michaud, 1838) should be synonymized with *B. alexandria* (Ehrenberg).[2]

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[1] Contribution from the Department of Zoology and the Museum of Zoology, University of Michigan, and the University of Khartoum, Sudan.

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[2] After this paper was submitted, a World Health Organization Technical Report Series 1954, No. 90 came out on "Bilharzia Snail Vector Identification and Classification (Equatorial and South Africa) Report of a Study-Group." The group compiled a tentative list of various species of *Biomphalaria*, but does not consider the classification final.

DESCRIPTION

The animals of the family Planorbidae are contained in sinistral shells which are usually discoidal or occasionally physoid. In studying the anatomy of snails it is best to use relaxed specimens. For this purpose relaxing agents, such as menthol, can be used. In all cases relaxation should be carried out before fixation.

The planorbid animal shows the generally recognized three divisions of the molluscan body: a head, a foot, and a visceral mass surrounded by a mantle. The head and the foot are fused to form the head-foot organ which is extended beyond the shell when the snail is active. The head-foot organ is somewhat triangular in outline. A pair of contractile tentacles, at the bases of which are a pair of eyes, protrude from its upper surface. The mouth is ventral. The male genital orifice is near the base of the left tentacle (Plate 1, fig. 1). This arrangement is in contrast to that found in the dextral Lymnaeidae (Baker 1911; Carriker 1946), where the genital orifices are on the right side of the head-foot organ. Along the edge of the shell aperture, the animal has a thick fleshy flap, the mantle collar, which surrounds the *neck* of the snail and embraces a pseudobranch. It is continuous ventrally with the columellar muscle and, dorsally and laterally, it extends as the mantle —a thin, soft, flexible structure surrounding the respiratory cavity and the visceral organs. The mantle, and particularly its collar, secretes the shell. The respiratory or pulmonary cavity is actually an extension of the mantle cavity lined by the respiratory epithelium, which is richly supplied with blood vessels. A large portion of the respiratory cavity is on the right side of the animal with the cavity connected to the air outside through an opening, the pneumostome, situated on the right side of the pseudobranch. The latter represents an outgrowth from the respiratory wall and functions like a gill in providing the animal with the dissolved oxygen in water. White mottling (due to concretions in the connective tissue) usually covers the head-foot organ as well as the rest of the body. Such concretions were also reported in *Helix* by Kisker (1923) and von Haffner (1923), in *Lymnaea stagnalis appressa* by Carriker (1946), in *Bulinus* by Hubendick (1948b), and in *Helisoma trivolis* and *H. anceps* by Abdel-Malek (1952a).

If the pulmonary cavity is opened, one observes the main part of the kidney adhering to its dorsal wall. In transverse section, this portion of the kidney reveals several renal lamellae in its cavity. The remainder of the kidney is a small distal[1] portion adhering to the left side of the pericardium and heart (Plate 3). These two parts of the kidney were referred to by Baker (1945) as *tubular* and *sacular*. However, histologically both parts are the same. It should be noted that the renal epithelium in the *tubular* portion is more undulated and that there are more tubules in the cavity of this portion of the kidney. The proximal end of the kidney terminates in a short, thick, tubular ureter (Plate 3), which curves on itself and opens into the respiratory cavity close to its proximal boundary.

The pericardium, containing an auricle and a ventricle, lies on the right side of the animal (Plate 2) in a concavity between the distal portion of the kidney and the albumen gland. Plate 1, fig. 1 shows the renal vein to the left of the kidney while the pulmonary vein is to the right. Blood is collected from

[1] The terms proximal and distal are considered in relation to the head-foot organ.

the body in a number of venous sinuses, often called *spaces* which join capillaries; it is then carried to the kidney and respiratory organs for purification and oxygenation. The renal vein collects blood from the kidney, while the pulmonary vein collects it from the pseudobranch and the lung, after which both veins proceed *distad* to enter the auricle (Plate 3). The heart pumps arterial blood into an aorta which gives off branches to various organs of the animal. The blood of Mollusca is often referred to as *haemolymph* or *lymph* and accordingly one comes across terms like *lymph spaces*, etc. In the planorbids, the blood contains haemoglobin dissolved in the plasma; hence its red color.

The mouth of the snail is surrounded by a jaw of three brown, horny plates, one upper (ja.) and two lateral. The buccal mass (b.m.) contains the radular ribbon supported by cartilage and operated by several muscles. A pair of salivary glands open into the buccal mass at its junction with the esophagus. These glands are elongate and extend for some distance along both sides of the esophagus. The edges of the glands appear fringed because they are made up of a large number of small lobes. The distal ends of the glands are often joined. Near the level of the base of the tentacles the esophagus is surrounded with a ring of nerve ganglia (Plate 3), which send out nerves to the various organs of the snail. The esophagus lies in the center of the head-foot organ and extends distally along the columellar muscle and continues adherent to the genitalia until it expands to form the proximal chamber of the stomach or crop (cr.) (Plate 3). The stomach is divided into three clearly defined parts: (1) the crop; (2) a large muscular portion or gizzard (gz.), usually with a silvery appearance and containing sand granules; and (3) the pylorus (py.) from which the intestine emerges. The pylorus also gives off a short, finger-like blind sac or caecum. The intestine (in.) emerges from the pylorus, curves around the stomach, then passes through the concavity of the albumen gland (Plate 1, fig. 1) and continues distally as a loop through the digestive gland. It then proceeds forward on the left side of the animal as the rectum (Plate 3) passing through the pseudobranch before opening to the outside at the anus. There is a broad, conspicuous ridge above the rectum, which is continuous with a fibrous covering on both sides of the rectum (part of this ridge is shown on Plate 4, fig. 3).

The liver, or digestive gland (d.g.), has a compound tubular arrangement. These tubules end blindly to form a mass of follicles with their supporting connective tissue. The organ occurs distad to the stomach and covers its posterior part. If a small part of the liver is removed, several thick, branching ducts can be seen ramifying through the liver tubules. These hepatic ducts unite to form a single tube which opens into the pyloric portion of the stomach close to the origin of the caecum. According to Baker (1945), variation in the digestive system among planorbids has been observed mainly in the form of the stomach.

The ovotestis (ovt.), or hermaphroditic gland, is a coiled organ located in the sunken spire of the shell. It is formed of several follicles or *acini* and only a small portion of it is covered by liver tissue. The mantle covers both digestive gland and ovotestis and is represented by a transparent membrane under which there is a layer of connective tissue well supplied with blood spaces (sinuses). This covering layer is the *tunica propria* of some authors. The products of the hermaphroditic gland are conveyed by a hermaphroditic

duct (h.d.) which is provided with seminal vesicles (s.v.) near the junction of the duct with the gland (Plate 3). A part of the liver tissue should be removed in order to see these vesicles. Near the cup-shaped albumen gland, the hermaphroditic duct divides into the male and female duct systems which proceed, adhering to each other, along the ventral side of the respiratory cavity.

In the male system the sperm duct arises as a bifurcation of the hermaphroditic duct. After receiving the secretion from the large prostate gland (pro.g.), the sperm duct becomes the vas deferens (v.d.), which forms a loop before it opens at the distal end of a *penial complex* in the head-foot organ. The prostate gland varies among the several genera of Planorbidae. In some forms the prostate tubules pour their secretion into a prostate duct which unites with the vas deferens. Hubendick (1948a) considered the prostate the secretory portion of the vas deferens. He also stated that in the Physidae, Ancylidae and Planorbidae the gland is different in appearance and histological structure from that of other Basommatophora (aquatic pulmonates). The penial complex consists of a distal portion, the vergic sac (v.s.), containing the verge within and a proximal preputium (pre.). Connolly (1925) called the preputium of *B. pfeifferi* a penis-sac. The preputium opens to the outside through the male genital orifice (m.g.o)., situated at the base of the left tentacle.

In the female system the oviduct arises also as a bifurcation of the hermaphroditic duct. It twists around the sperm duct and then leads into a thick-walled compressed uterus (ut.), which adheres to the prostate gland and continues as the vagina, opening into the female orifice (f.g.o.), situated beneath the left portion of the pseudobranch.

Of the various organ systems, the genitalia exhibit the most distinct variation among the genera and species in the family Planoribidae. These genital differences are also pronounced in other groups of pulmonate snails. These differences appear to be more noticeable in male organs than in the female. In this connection, details in the gross anatomy and histology of the genitalia of two other planorbids, *Helisoma trivolvis* Say and *B. biossyi* (Potiez et Michaud), appeared in two earlier papers (Abdel-Malek, 1954a and 1954b).

Faust and Hoffman (1934), quoting a letter from F. C. Baker, stated: "What you call a septum in the Planorbidae is in reality a bag or sac which encloses the entire posterior part of the body of the animal . . . it separates the two parts of the body and for your purposes is a real septum or division. . . ." This assertion is only partially true. Actually no septum or division exists between the proximal and the distal portions of these snails. Many planorbid snails have been carefully examined both by gross dissection and in studies of serial sections. Evidently the so-called septum reported by Faust and Hoffman is really only a membrane which forms the distal limit of the respiratory sac (plate 3). That membrane covers a part of the albumen gland and then continues as a membranous covering of the male and female genital tracts and other organs. Obviously this so-called septum does not form a complete barrier extending from the dorsal to the ventral surfaces of the snail as illustrated by Faust and Hoffman (1934). Consequently, the distal part of the viscera is not completely separated from the proximal. That distal portion, i.e., the region containing the ovotestis, digestive gland, stomach, intestine, and albumen gland (Plate 3) is definitely continuous underneath and connects on both sides of the alleged septum with the proximal organs, such as the rectum, the male and female duct systems, and the esophagus. The continuity of both

the proximal and the distal visceral organs can be traced through the head-foot organ where the esophagus is connected to the buccal mass and the genital ducts reach the genital orifices.

OBSERVATIONS ON MIGRATION OF S. MANSONI IN BIOMPHALARIA BOISSYI

A detailed treatment is unnecessary since certain aspects of such migration have already been investigated by several others. Faust and Hoffman (1934), Maldonado and Acosta Matienzo (1947), and Olivier and Mao (1949) discussed the movement of *S. mansoni* in the snail *Australorbis glabratus;* they also contributed considerable detail on the structure of the successive larval stages. La Rue (1951) discussed various aspects of the migration of the larval forms of several groups of trematodes within the snail intermediate hosts.

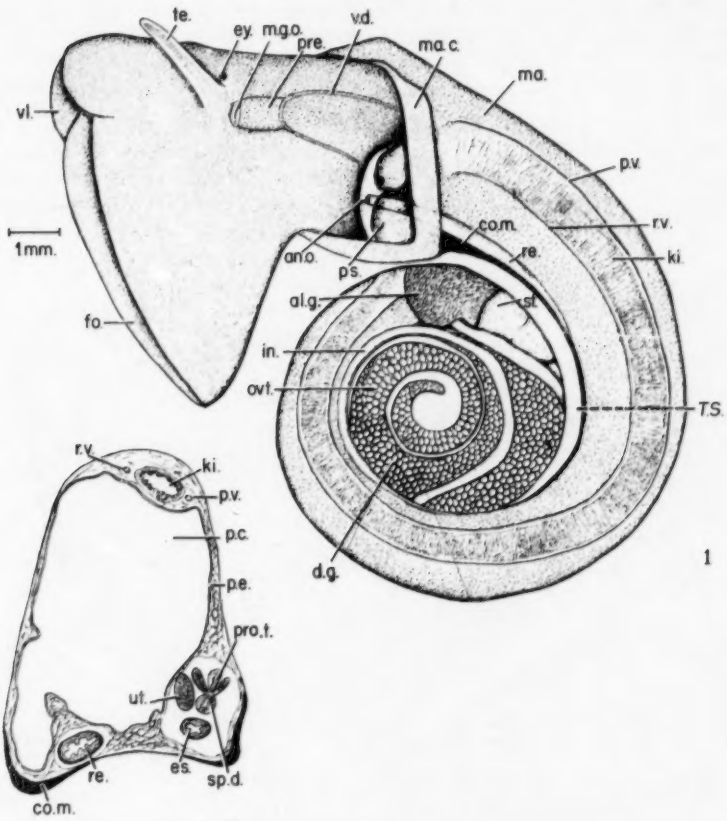
Miracidial cultures were obtained by the method of McMullen and Beaver (1945). Exposures of the snails to the miracidia, the reaction of these miracidia to the snails, and observations on the sites of penetration into the snail, all those phases were previously discussed (Abdel-Malek, 1950). Single snails were exposed in small stender dishes (30 mm in diameter) but *en masse* exposures were carried out in finger bowls. With both methods the snails were placed in relatively small amounts of water. Plate 3 serves as a guide for tracing the various sites in which the larval stages of *S. mansoni* were observed. Miracidia penetrated the tentacles (te.), the head-foot organ, and all the exposed surface of the snail extending as far as the mantle collar (ma.c.). It was evident that the miracidia *drilled* through the epiderm of the snail, apparently aided by secretions from their penetration glands. Miracidia observed after penetrating young snails reached the blood spaces and the surrounding connective tissue beneath the skin. Several miracidia showed little motion due to exhaustion after penetration, while a few still active ones moved aimlessly. Some of them may move to the distal part of the head-foot organ. Olivier and Mao (1949) recovered four mother sporocysts of *S. mansoni* from the visceral mass of *Australorbis glabratus,* three from the respiratory membranes and one from the surface of the stomach. Sectioned animals showed that the majority of the miracidia develop near the sites of penetration. The miracidia became mother sporocysts within three to four days after penetration when they appeared as elongated thin-walled sacs, containing germ cells. These mother sporocysts were observed in the tentacles, near the nerve ganglia (n.g.), and esophagus (oes.), in other parts of the head-foot organ, and in the pseudo-

ABBREVIATIONS USED IN PLATES

ac.—acini; al. g.—albumen gland; an. o.—anal opening; au.—auricle; b. m.—buccal mass; co. m.—columellar muscle; d. g.—digestive gland; es.—esophagus; ey.—eye; f. g. o.—female genital opening; fo.—foot; gz.—gizzard; h. d.—hermaphroditic duct; in.—intestine; ja.—jaw; ki.—kidney; ma.—mantle; ma. c.—mantle collar; m. g. o.—male genital opening; mu. g.—muciparous gland; n. g.—nerve ganglia; ovd.—oviduct; ovt.—ovotestis; p. c.—pulmonary cavity; p. e.—pulmonary epithelium; pe. ca.—pericardial cavity; po. al. g.—position of albumen gland; pre.—preputium; pro. g.—prostate gland; pro. t.—prostate tubule; ps.—pseudobranch; p. v.—pulmonary vein; py.—pylorus; re.—rectum; r. v.—renal vein; s. r. s.—seminal receptacle sac; sa. g.—salivary gland; sp. d.—sperm duct; spo.—sporocyst; st.—stomach; s. v.—seminal vesicles; T. S.—transverse section; te.—tentacle; ur.—ureter; ut.—uterus; v. d.—vas deferens; v. s.—vergic sac; ve.—verge; ven.—ventricle; vl.—velum.

branch (ps.). The motile daughter sporocysts, formed inside the mother sporocysts, apparently ruptured the mother sac and migrated. Observations on the course of this migration revealed that some daughter sporocysts moved to the neighborhood of the vergic sac (v.s.), into the pulmonary wall, the tissues of the kidney (ki.), the heart (au. and ven.), the pericardial wall, around the rectum (re.), and along the genital tract (ovd., sp.d. and ut.) and esophagus (oes.). Other daughter sporocysts continued their migration distad and reached the region of the digestive gland (d.g.) and ovotestis (ovt.). They

PLATE 1



Figs. 1, 2.—1. View of left side of *Biomphalaria boissyi*, drawn after removing the shell. Preserving the animal for a long time in ten percent formalin caused the pigmentation of the mantle (ma.) to fade and as a result several visceral organs, as well as the vas deferens (v.d.) and preputium (pre.) in the head-foot organ, became more readily visible. 2. Transverse section (T.S.) through the animal showing the interrelation of organs in the region of the transect (fig. 1). The pulmonary cavity (p.c.) is lined with epithelium (p.e.) and is surrounded dorsally by the kidney (ki.) and ventrally by the genital organs, esophagus (es.) and rectum (re.).

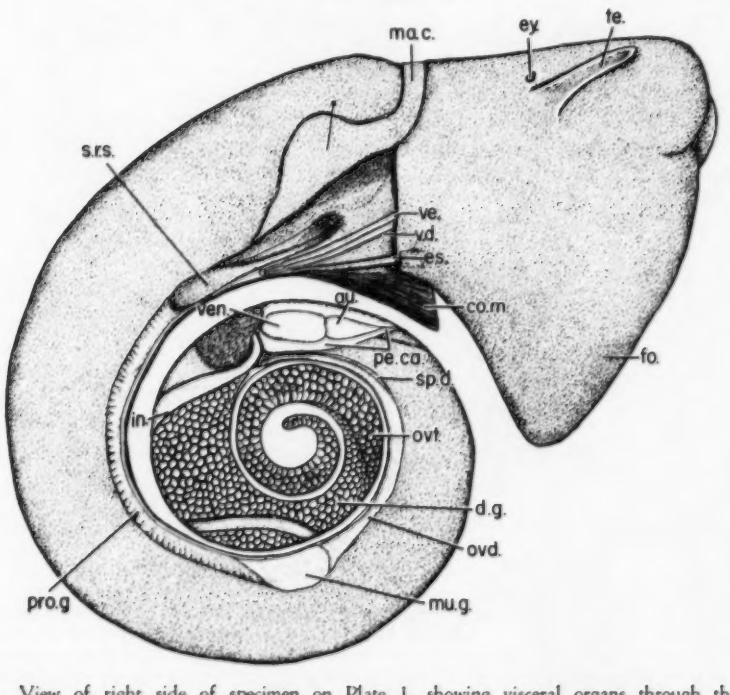
were found in the connective tissue between the tubules of the digestive gland, the acini of the ovotestis, and in the connective tissue layer (part of the mantle) surrounding these structures. Evidently it is this connective tissue around and between the tubules and acini which provides a suitable medium for further development of the parasite. It is of interest to note that daughter sporocysts of *S. mansoni* were never observed inside the tubules of the digestive gland or the acini of the ovotestis, but they were always in between them (Plate 4, fig. 2). Although the sporocysts were apparently unable to penetrate the latter tubules or the acini, they did exert marked pressure on them.

After the cercariae emerged from the daughter sporocysts they left the snails and swam in the water. Experimentally infected snails shed cercariae after 28 to 34 days from the time of exposure to the miracidia.

DISCUSSION

The gross morphology of a planorbid snail, *Biomphalaria boissyi*, as it is given here, is intended to serve as a guide for a better understanding of snail-parasite relations. Faust and Hoffman (1934) asserted that a definite septum completely splits the visceral mass into a proximal and a distal portion, and

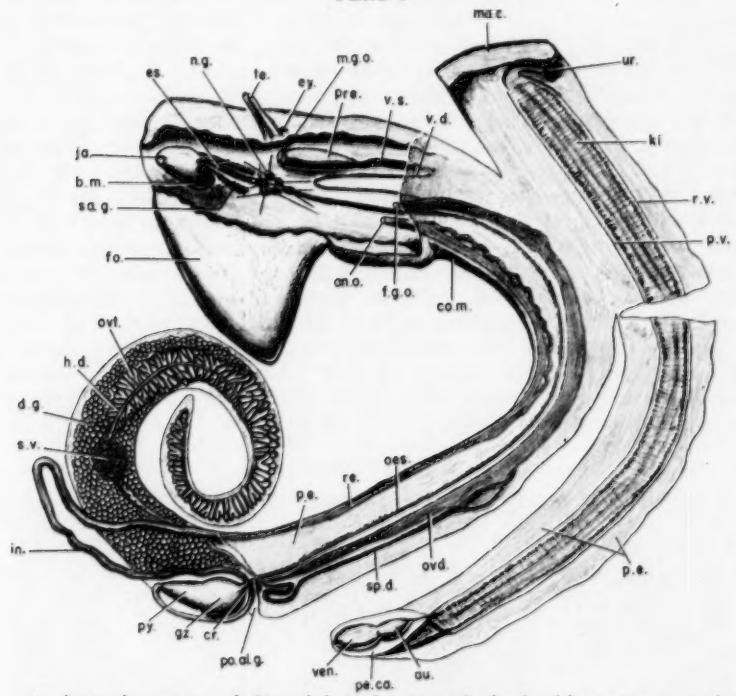
PLATE 2



View of right side of specimen on Plate 1, showing visceral organs through the mantle. Part of the mantle collar (ma. c.) is turned up to show a portion of the verge (ve.), vas deferens (v. d.), and esophagus (es.).

that in schistosomes, as in other trematode infections, development of the parasites occurred in the distal region surrounding the digestive gland where there is a loose lymphatic fluid. They stated that if it were not for the delimitation of such a distal region, one might expect to find sporocysts and immature cercariae distributed through the more proximal as well as in the more distal visceral mass. However, as this anatomical study has shown, the proximal and the distal viscera of *B. boissyi* are continuous and daughter sporocysts of *S. mansoni* were observed in proximal organs, such as the kidney, the respiratory epithelium, around the rectum, near the prostate, uterus, and sperm duct, etc., as well as in or near distal organs. Also, a study of the infections of the snail *Helisoma corpulentum* Say with the echinostome *Petasiger chandleri* Abdel-Malek, 1952b indicates that daughter rediae occur in proximal organs, (prostate gland, heart, kidney, and around the rectum), as well as in distal organs (digestive gland and ovotestis).

PLATE 3

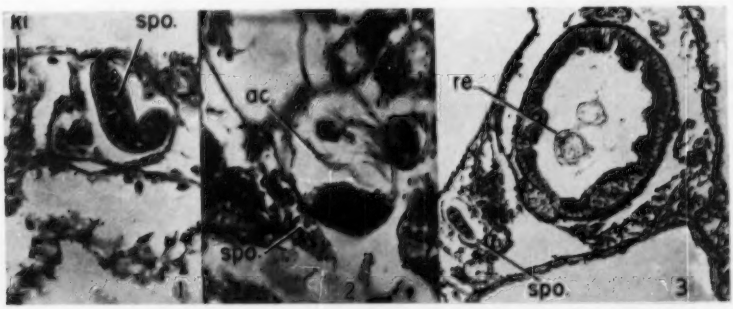


A dissected specimen of *Biomphalaria boissyi*, with the head-foot organ opened to expose internal organs; the respiratory cavity is laid open and, accordingly, the pulmonary vein, which lies on the right side of the kidney, is shown on the left side. Muscles supporting the buccal mass (b. m.) and preputium (pre.) are not shown. The fused distal portions of the salivary glands (sa. g.) are separated to expose the esophagus (es.). The albumen gland is removed to reveal the crop (cr.), a part of both gizzard (gz.) and intestine (in.), as well as the distal limits of the respiratory cavity, which has been referred to as a septum by some authors. The esophagus, normally underneath the genitalia, is pushed to one side so that it can be observed through the pulmonary epithelium (p. e.). Genitalia and rectum are ordinarily visible through the epithelium.

The significance of the migration of *S. mansoni* and other trematodes through their intermediate snail hosts is also of interest. No complete nor conclusive explanation of the reason for this migration has yet been presented. La Rue (1951) speculated that the migration distad of daughter sporocysts of trematodes from the proximal locus where they are formed inside the mother sporocyst may represent a change of host that might have occurred early in the evolutionary history of the Digenea. Van der Woude (1954) expressed a similar view in the case of *Megalodiscus temperatus* where the three generations of rediae occur in different zones of the host, *Helisoma trivolvis*. Additional interpretations regarding the migratory course are indicated in this anatomical study. It is very likely that daughter sporocysts of *S. mansoni* do not maintain a special course of migration but either migrate at random by their own movements, or are carried to various organs by the circulating hemolymph. It is established that the distal organs, with their spacious connective tissue and blood spaces, harbor the majority of the daughter sporocysts and a smaller number can be accommodated in proximal organs.

The place where the miracidium settled after penetration determined the position of the mother sporocyst developing from it since the latter is non-motile. It was found that the majority of the miracidia settled close to the site of entry in the exposed head-foot organ, mantle collar and pseudobranch. The daughter sporocysts develop motility and are capable of migration. They evidently move at random in all directions since some daughter sporocysts were found in various proximal parts of the head-foot organ. Maldonado and Acosta Matienzo (1947) observed the wandering of the daughter sporocysts of *S. mansoni* and they suggested that the parasite is not guided toward the digestive gland by any true sense of direction. Presumably the daughter sporocysts would pass through the respiratory epithelium, through the tissues surrounding the esophagus, rectum, and genitalia and proceed along the distal portion of the respiratory cavity until they reached the stomach, albumen gland, digestive gland, and ovotestis. That there is no barrier to their migration and that the visceral structures are continuous along the distal portion of the respiratory cavity has already been indicated. Consequently, some of the daughter sporo-

PLATE 4.



Figs. 1-3.—1. Daughter sporocyst (spo.) of *S. mansoni* inside kidney (ki.); 2. Daughter sporocysts in the connective tissue layer between the acini (ac.) of the ovotestis. No sporocysts are found inside the acini. Notice large mature ovum inside the acinus. 3. Daughter sporocysts in the ridge around and above the rectum (re.).

cysts settle in proximal organs, e.g., kidney, rectum, respiratory epithelium, and around the genitalia and they do not continue movement toward distal organs. However, the distal organs are provided with spacious connective tissue around and between the tubules of the digestive gland and also the acini of the ovotestis contain an ample nutritive supply for the daughter sporocysts and the cercariae developing later inside them. It is quite possible that in heavy infections some of the daughter sporocysts may move back from distal organs to more proximal ones.

These studies lead me to believe that many daughter sporocysts occur in distal organs, far from the proximal position of the mother sporocysts, because they are carried there by circulating blood in its normal route. As already indicated, the blood is collected from various organs of the snail in venous spaces which lead to thin capillaries. Some daughter sporocysts because of their motile nature move into blood spaces. Once in the circulating blood they would migrate from proximal organs distad to the lung, pseudobranch and kidney; they could remain in any of these organs along the way. Since the blood continues to flow distad within the renal and pulmonary veins, daughter sporocysts may be carried to the heart, and they could then be distributed by the branches of the aorta to such distal organs as the stomach, albumen gland, intestine, digestive gland and ovotestis, as well as to proximal organs. The daughter sporocysts found in the heart might have been some that were passing through it. It is well established that the distal organs with their spacious connective tissue and numerous blood spaces provide the medium and nutrition necessary for the maintenance and development of many daughter sporocysts; the proximal organs, which have large amounts of muscle tissue but are poor in connective tissue compared to the distal organs, usually harbor smaller numbers of daughter sporocysts.

SUMMARY

A detailed description of the anatomy and the relationships of the organ systems of *Biomphalaria boissyi*, a typical planorbid snail, not only provides information of malacological importance, but also serves in tracing the migration of *Schistosoma mansoni* through its planorbid intermediate host. A previous claim that a structural barrier prevents migration of the parasitic larval stages from proximal and distal organs is shown to be erroneous. The daughter sporocysts may either migrate at random by their own movements, or they can be carried by circulating blood to various organs. The occurrence of most daughter sporocysts in distal organs is associated with the fact that those areas structurally represent the most favorable environment.

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The Anatomy of the Gnathosoma of Pergamasus vargasi n. sp.[1] (Acarina—Mesostigmata —Gamasides)

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In the present paper, which is one of a series of studies on the gnathosomal structures of the mesostigmatid acarina, the feeding apparatus of the gamasid mite, *Pergamasus vargasi* is described and figured. About thirty specimens of this mite were collected by H. Rolund in March and July of 1948 from the nests of *Microtus* sp. in Venango and Warren Counties, Pennsylvania. The specimens were not immersed in a fixing solution so satisfactory sections of the mites were not possible. The present study is made from whole mounts and from dissections of the gnathosoma. The methods used are the same as described in a recent paper on *Megisthanus floridanus* (Gorirossi and Wharton, 1953).

Börner published in 1903 *Die Mundbildung bei den Milben.* In this magnificent study he attempted to homologize the mouth parts of the Arachnoidea with those of the Acarina. He chose what he considered to be a primitive type, *Pergamasus crassipes,* to illustrate the similarity between the two groups. The details of this classical piece of work need not be of concern here. The main point of interest for the moment is in the terminology he used for the various gnathosomal parts. Börner's figure 4 of *P. crassipes* (fig. L) is included in the present paper in order to compare the gnathosomal structures of *P. crassipes* with those of *P. vargasi.*

Acknowledgement.—The author wishes to express her thanks to Dr. G. W. Wharton of the University of Maryland for his helpful advice and criticism.

Gnathosoma.—The gnathosomas of the male and female of *P. vargasi.* are in general essentially similar and yet in some details strikingly different. In the male the hypostomal region is more clearly differentiated from the protosternal region; the hypostomal processes of the male are more pronounced than those of the female; and the teeth on the hypopharyngeal processes are more extensive in the male than are those of the female. The chelicerae are the structures which offer the most outstanding differences between the sexes.

The gnathosomal ring of both sexes is circular in outline and heavily

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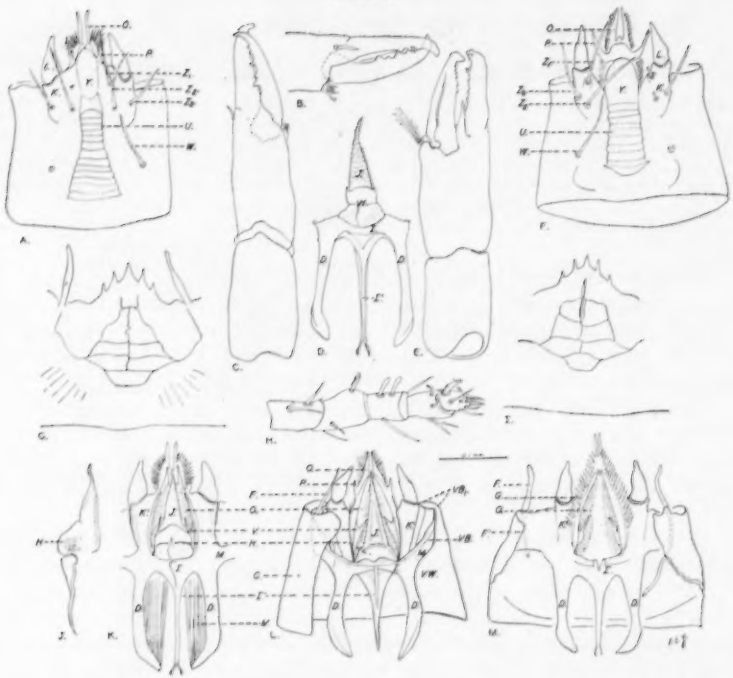
[1] The naming of animals is one branch of zoology where it is at times necessary to make a conclusion before all of the pertinent facts are at hand. The naming of this species is a case in point. *P. vargasi* has been compared with descriptions of a number of other species of *Pergamasus* and has been found to differ from the descriptions and/or the figures of previously described forms. The form described in this paper is named in honor of Dr. Luis Vargas of Mexico. The type specimen will be deposited in the U. S. National Museum.—G. W. Wharton.

[2] This project was supported by ONR contract N7-ONR-45506 at Duke University, Durham, North Carolina.

PLATE I.



(A-K, M) Gnathosomal structures of *Pergamasus vargasi*. (L) Gnathosomal structures of *Pergamasus crassipes*.—A. Ventral view of the female; B., C. Medial and lateral view of chelicera of female, respectively; D. Dorsal view of epipharynx and labrum to show relationship with epistome, posterior epistomal process and bars of subcheliceral plate; E. Lateral view of chelicera of male; F. Ventral view of male; G. Ventral view of tectum of female to show relationship with salivary styli; H. Palp; I. Ventral view of tectum of male; J. Lateral view of epipharynx to show relationship with labrum and posterior epistomal process; K. Dorsal view of gnathosoma of female with tectum, chelicerae and cheliceral sheaths removed; L. Same as K (after Börner); M. Dorsal view of gnathosoma of male with tectum, chelicerae, cheliceral sheaths, labrum and epipharynx removed—note hypopharyngeal teeth (g). Scale is applicable to all figures except L.

LIST OF ABBREVIATIONS USED IN PLATE: C, *Carapax* (after Börner); D, subcheliceral plate (*coxales Apodem*); F, salivary stylus; F′, duct of salivary gland; G, dorsal row of hypopharyngeal teeth; H, labrum (not designated by Börner); I, epistome; I′, posterior epistomal process (*labrales Apodem*); J, epipharynx (*Labrum*); K, hypostome; K′, dorsal wall of hypostome (*dorsalen Wand der Coxa*); L, corniculus (*Dorn der Coxa*); M, tentorium; O, hypopharyngeal process (*Coxopodit*); P, hypostomal process (*not labeled*); Q, hypopharyngeal wall (*unter (hintere) Pharynxlamelle*); U, deutosternum; V, hypopharyngeal stylus (*lappiger Anhang der Coxa der 2 Extr., die Mündhohle von oben theilweise bedeckend*); W, gnathosomal seta; Z_1, $_2$, $_3$, distal, medial and lateral hypostomal setae; VW, *ventrale Wand der Coxa* (after Börner); VB, *Verbindungshaut zwischen dem Carapax und der Coxa* (after Börner); VB_1, *Verbindungshaut von Coxa und Trochanter der 2. Extremität* (after Börner).

sclerotized. It projects from the anteroventral surface of the elliptically-shaped idiosoma; its posteroventral margin is just anterior to coxae I.

Gnathosomal base.—(A, F) The posterior two-thirds of the gnathosoma is the gnathosomal base. Except for the gnathosomal setae and the deutosternum it is devoid of ornamentation.

Deutosternum.—The deutosternum (u) in the female (A) is 147 microns long. Its anterior edge is at a level between the distal and the medial hypostomal setae and its posterior edge is between the level of the gnathosomal setae and the posteroventral edge of the gnathosoma. It is narrow anteriorly and gradually widens posteriorly. Traversing it is a series of parallel ridges. They vary in number from twelve to sixteen. In most specimens the most posterior of these ridges usually contains a series of anteriorly projecting, triangularly-shaped teeth. The presence of these teeth or their number is not consistent in different specimens. Some have been found in which only the most posterior ridge is provided with teeth.

The deutosternum of the male (F) is not as long as that of the female. It measures 107 microns long. Its anterior edge is at the same level as the medial hypostomal setae and its posterior edge is between the level of the gnathosomal setae and the posteroventral edge of the gnathosoma. As in the female, there are ridges which traverse its surface, and these vary from nine to twelve in number. The deutosternal teeth in the male are more numerous and more pronounced than those in the female.

Gnathosomal setae.—The gnathosomal setae (w) of the female are shorter (92 microns) than those of the male (101 microns). In both sexes they have numerous setules and are directly posterior to the lateral hypostomal setae.

Horizontal shelf—(D, K, M) The horizontal shelf composed of the epistome (i), tentorium (m) and subcheliceral plate (d) has an additional component which projects between the two bars of the subcheliceral plate. It is a lightly sclerotized bar (i′) which originates from the mid-posterior surface of the epistome and extends beyond the tips of the bars of the subcheliceral plate.

Epistome.—The epistome is a narrow, sclerotized bar (i) from which the labrum (h) projects anteriorly. From its midposterior surface arises the posterior epistomal process (i′) just described. This epistomal process measures 175 microns in the female and 129 microns in the male. Epipharyngeal muscles originate from this process as well as from the posteroventral surfaces of the bars of the subcheliceral plate.

Tentorium.—The tentorium (m) is the same as described for *M. floridanus.*

Subcheliceral plate.—Unlike the bars of the subcheliceral plate in previous studies on the gnathosoma of the Mesostigmata, the bars (d) in *P. vargasi* are not connected proximally. They are, however, held rigid by the internal cheliceral sheaths which connect the lateral sides of the bars of the subcheliceral plate with the lateral sides of the epistomal process (i). The bars of the cheliceral plate are 123 microns long in the male and 169 microns long in the female.

Cheliceral sheaths.—The external and internal cheliceral sheaths are the same as those described for *M. floridanus.* Whereas, however, in *M. floridanus*

the internal cheliceral sheaths are contiguous along their medial surfaces, in *P. vargasi* they originate from the medial sides of the bars of the subcheliceral plate (as in *M. floridanus*) and insert on the lateral sides of the epistomal process. The sheaths then originate from the distal surface of the process and continue dorsally and laterally to insert on the lateral surfaces of the bars of the subcheliceral plate, as *in M. floridanus*.

Pharynx.—The pharynx is triangular in cross section. The muscles which insert on its walls are similar to those described for *Bdellonyssus bacoti* (Gorirossi, 1950).

Tectum.—The tectum of both sexes is quite similar. Its distal edge terminates in five teeth which are larger in the female than in the male. There is a median tooth flanked on either side by two additional pairs of teeth; they are all about equidistant apart. The tectum of the male (I) measures 256 microns from tip to base and that of the female (G) measures 161 microns. The dorsal surface of the tectum is delicately sculptured with a series of lines which intersect each other so that the pattern resembles a series of blocks. In one male and one female specimen there were seven such blocks. The sculpturing is also clearly visible from a ventral view. From the mid-ventral surface of the tectum of the male extends a slender, sclerotized flap which is 70 microns long. This flap is absent in the female.

Epipharynx.—(D, J, K) The epipharynx (j) is 123 microns long. Its mid-ventral surface is more heavily sclerotized than its walls. It is covered with tiny, triangularly-shaped spines.

Labrum.—(D, J, K) The labrum (h) cannot be separated from the dorsal wall of the epipharynx. It is, however, easily discernable from a lateral view. It covers approximately the dorsal, posterior third of the epipharyngeal wall and when extended resembles a spread wing (J). Its outline is difficult to discern from a dorsal view.

Hypopharynx.—(K, M) The hypopharyngeal walls (q) are lined with a series of spines which cover it from anterior to posterior end. The walls in the female terminate in two needle-like projections which lie just dorsal to the hypopharyngeal processes. Those of the male terminate in shorter, rounder projections. The sexes can be easily differentiated from a study of the hypopharynx. In the male (M) the dorsal edge of the hypopharynx is lined with a fringe of long, hypopharyngeal teeth (g) similar to those described for the Celaenopsina (Gorirossi, 1955b). These are continuous anteriorly with the hypopharyngeal processes. In the female, on the other hand, this dorsal fringe of teeth is absent from the dorsal wall of the hypopharynx.

Hypopharyngeal processes.—(A, F) The hypopharyngeal processes (o) of the female project anteriorly beyond the distal tip on the protosternum. They can be differentiated into two regions: the more conspicuous and distal portion is composed of a pair of long, lightly sclerotized, blade-like structures which are continuous proximally with the finger-like processes. This fringe of finger-like processes radiate on either side of the protosternum. Dorsally, these processes terminate just anterior to the distal tip of the hypopharynx. In the male the posteroventral edge of the hypopharyngeal processes are contiguous with the anteroventral edge of the hypostomal processes. The blade-like struc-

tures fuse proximally and their lateral edges are deeply fringed. The fringes or teeth extend the length of the hypopharynx and border it dorsally.

Hypopharyngeal styli.—(K, M) The hypopharyngeal styli (v) arise from the posterior portion of the dorsolateral walls of the hypopharynx and project dorsally over the epipharynx. They are slender, lightly sclerotized, thumb-like projections which curve medially. They measure approximately 30 microns long.

Hypostome.—(A, F) The hypostomal region (k) of the male is clearly differentiated from the protosternum. The walls appear almost oval in shape and project obliquely on either side of the protosternum. Projecting from their distal surfaces are the corniculi and from their ventral surfaces the hypostomal setae. The hypostomal region of the female is similarly characterized, but there is no sharp differentiation between the walls of the protosternum and the walls of the hypostome.

Hypostomal setae.—(A, F) The distal (z_1), medial (z_2) and lateral (z_3) hypostomal setae of the male measure 86, 123 and 89 microns, respectively. Those of the female measure 98, 123 and 92 microns, respectively. In both sexes the medial and the lateral setae possess setules and the distal setae are nude. In the female the setae are so arranged that each occupies the angle of a right triangle, the hypotenuse of which connects the distal and the lateral setae. In the male the hypotenuse connects the distal and the medial setae.

Protosternum.— (A, F) The protosternum (y) of the male is longer and wider than that of the female and its anterior two-thirds projects freely between the medial walls of the hypostome. In the female the protosternum is narrower than that of the male and its lateral walls are contiguous with the medial walls of the hypostome. In both sexes it is easily discernible from the deutosternum which is continuous with it posteriorly.

Hypostomal processes.—(A, F, K) The hypostomal processes (p) of the male are just anterior to the protosternum and originate from the medial sides of the hypostome. They resemble a pair of horns projecting on either side of a bridge between them. The ends of the *horns* may terminate in a single point or they may be split several times. In the female each of the slender, horn-like hypostomal processes project anteriorly from the medial, distal surface of the ventral wall of the hypostome. The hypopharyngeal processes are more dorsal in position and project behind them. In the male the hypostomal processes measure 46 microns long and in the female 49 microns long.

Corniculi.—(A, F, K, M) The corniculi (1) are heavily sclerotized, horn-like structures which project from the distal surface of the hypostome and curve slightly medially. In the male they measure 67 microns long and in the female 70 microns.

Chelicerae.—(B, C, E) The chelicerae of the male and the female of *P. vargasi* show more sexual dimorphism than any of the other gnathosomal structures. Those of the female (C) are more slender and longer than those of the male (E). In the female the first segment is subequal in length with the second segment. The immovable digit has four teeth (more or less in different specimens) restricted to the anterior half of the digit. At the base of the digit (B) on its medial side is a large, graceful seta. Also on its medial side is a tiny seta between its anterior two teeth. The movable digit of the female has five

teeth on most specimens examined. At the base of the digit the synarthrodial membrane resembles an expanded balloon with a corona of anteriorly projecting, lightly sclerotized, needle-like projectings encircling it posteriorly. The chelicerae of the male are more robust than those of the female. The first segment is narrower and shorter than the second segment. The two setae present on the immovable digit of the female are present also on the immovable digit of the male. The immovable digit has from seven to nine teeth on its cutting surface, none of which are well developed, but look more like small, projecting knobs. The movable digit has from seven to nine similar teeth on its cutting edge. It is split into two, slender portions. The split extends from the base of the digit to about a fourth of the distance from its tip. The needle-like projections encircling the synarthrodial membrane at the base of the movable digit are more slender and about five times longer than those at the base of movable digit in the female.

Pedipalps.—(H) The relative length of the five segmented palps range in size as follows: 2:3:5:4:6. The trochanter is a relatively long, slender segment with two setae on its medial surface and a short spine which projects from its medial, distal edge. Both setae have tiny setules at their tips. The setae are sharp and rigid. The more anterior of the two is the longer. The femur has 5 setae: 1 medial, 1 ventral and 3 dorsal. The one seta on its medial surface is curious in that it is not slender and pointed as most but is broad and flat and extremely thin. Extending from its ventral surface are tiny setules. The ventral seta is short and curves sharply laterally about midway along its length. It has a few setules at its tip. The three dorsal setae are subequal in length, longer than the others and nude. The genu has 5 setae: 2 medial, 1 lateral and 2 dorsal. The two medial setae are similar to the medial seta on the femur but lack the setules. The other three setae are long, slender and nude. The tibia has at least 11 setae: 2 ventral, 4 dorsolateral and 5 dorsal. All the setae on the tibia are subequal in length and nude. The two ventral setae curve posteriorly and the remaining eight are directed anteriorly. The tarsus has a crown of at least eleven, slender, curved, nude setae at its tip, two slender, nude setae on its ventral surface and the characteristic three-tined seta on its medial surface. The three tines of the seta are subequal in length but not in width. The two lateral tines curve slightly medially and have sharp points; the central tine is broad and flat and fits between the two lateral tines. The seta curves anteriorly, so that its proximal surface resembles the palm of a hand.

Salivary styli.—(G, M) The position of the salivary styli of *P. vargasi* recall those of *U. agilans* (Gorirossi, 1955a). They are slender processes which project over the chelicerae on either side of the tectum. They measure 92 microns long in the female and 77 microns long in the male.

DISCUSSION

As indicated in the introduction, Börner (1903) in his work, *Die Mundbildung bei den Milben,* was interested in establishing a relationship between the Acarina and the Arachnoidea. To do this he limited his study only to those Arachnoidea in which "the coxae of the second extremity (the pedipalps) help in building the mouth structures". His paper is invaluable for its critical study on the components of the mouth parts of the Arachnoidea.

At no time is the reader at a loss for interpreting exactly what Börner had in mind for his illustrations are unique in their clarity and aptness. From his study he found that Pedipalpida (exclusive of the Amblypygi) were the most closely related to the Acarina and to the "Gamasus group" in particular. This "Gamasus group" he considered primitive and took for his example the species *Pergamasus crassipes* (L). He reasoned that the only essential difference between the two groups is that in the Acarina the coxae of the pedipalps fuse with the carapace, whereas in the Uropygi this degree of fusion is never reached. Another morphological bridge between the two groups is that in the Pedipalpida the coxae of the pedipalps have moved dorsally and medially and eventually are contiguous with the lateral walls of the "labrum" (the labrum as defined by Börner = the epipharynx as used here). In the Acarina this association of the coxae with the epipharynx is retained by "coxal apodemes" (the subcheliceral plate as used here) and the coxae, as just stated, have fused with the "carapace" (the result of this fusion would be the gnathosomal ring). A significant fact that should be mentioned and which Börner thought important to substantiate his hypothesis is the presence in the Uropygi of what Börner refers to as the "medial or labral apodeme" (comparable to the posterior epistomal process (i') of *P. vargasi*). This apodeme, he states, may be suppressed or it may be present. The presence of a comparable structure in *P. crassipes* was significant to Börner for he felt that it represented a primitive condition and, therefore, reasoned that *P. crassipes* was primitive. His conclusion, a logical one from his point of view and perhaps the correct one, is that since the structures of the Arachnoidea and of the Acarina are not essentially different there is no reason for using different names for the structures found in the Acarina. Insofar as Börner's studies on the mouth parts of the Acarina went we find this is true, but there are certain structures which are present in other groups of Acarina which Börner did not mention. Among these are the hypopharyngeal styli (as found in *M. floridanus*), the epipharyngeal styli (found in *E. latus*), the salivary styli (as found in *P. crassipes*, which Börner did not label or discuss), and the labrum (as found in *M. floridanus* or *E. latus*, where it is a distinct morphological entity, readily seen and not as closely associated with the epipharynx as it is in *P. crassipes* and *P. vargasi*). Börner, as already stated, used the term labrum for the structure now referred to as the epipharynx. In his synonymy of terms he listed the term epipharynx as a synonym of labrum but did not explain why he chose to use labrum instead. Perhaps the reason is that he never studied a species in which the labrum projects separately and distinctly from the epistome.

Except for these rather minor discrepancies Börner understood completely the gnathosomal elements of the Acarina even to the point of mentioning the muscles which originate from the bars of the subcheliceral plate and insert within the epipharynx (his labrum).

One of the modifications found in the gnathosomal structures of *P. vargasi* is the means of strengthening the bars of the subcheliceral plate. It will be recalled that in the other species thus far studied, these bars are connected posteriorly by a lightly sclerotized bridge. In *P. vargasi* this bridge is absent, the tips of the bars terminate separately and their medial surface tilt dorsally. However, the posterior limit of the posterior epistomal process extends beyond the tips of the bars; the cheliceral sheaths, which in the other forms originate only from

the medial and lateral surfaces of the bars of the subcheliceral plate, in *P. vargasi* bridge the tiny space between the medial surfaces of the bars of the subcheliceral plate and the lateral surfaces of the epistomal process. Thus, the process would not only serve for the insertion for the sheaths of the chelicerae but also provide resistance to any movement of the bars of the subcheliceral plate.

One other noteworthy difference in *P. vargasi* is the meager development of the hypopharyngeal styli. They look like remnants of sclerotized material and are in no way comparable in development to the styli in the other forms studied.

As yet little can be said of the relationship of *P. vargasi* or *P. crassipes* to the other Gamasides for too few have been studied. Even less can be said of their being either primitive or specialized. What can be said is that their gnathosomal structures can be homologized with the gnathosomal structures of the Acarina thus far used in this comparative study of the gnathosoma of the Mesostigmata.

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BÖRNER, C. 1903—Arachnologische studien. V. Die Mundbildung bei den milben. Zool. Anz. 26:99-109.

GORIROSSI, FLORA E. 1950—The mouth parts of the adult female tropical rat mite, *Bdellonyssus bacoti* (Hirst, 1913) Fonseca, 1941 [= Liponissus bacoti (Hirst)], with observations on the feeding mechanism. J. Parasit. 36:301-318.

———1955a—The anatomy of the feeding apparatus of *Uropoda agitans* Banks, 1908, a mesostigmatid mite. Amer. Midl. Nat. 53(1):146-155.

———1955b—The gnathosoma of the Celaenopsina, (Acarina - Mesostigmata). Ibid. 54(1):153-167.

——— AND G. W. WHARTON 1953.—The anatomy of the feeding apparatus of *Megisthanus floridanus* Banks, 1904, a large mesostigmatid mite. Ibid. 50(2):433-447.

A List of Cestode Parasites From California Mammals[1]

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This report brings together information on the occurrence and distribution of cestode parasites in California mammals. The original information reported herein, was obtained by students, myself, and other staff members of this university. Although the host-parasite list which follows is far from complete, the dearth of knowledge about the helminth fauna in California seems to justify the publication of relatively few data, in the hope that other workers will be able to use this list as a starting point and add to it.

With few exceptions, the common names of the hosts, as given in the host list, were obtained from Burt and Grossenheider (1952). The keys and descriptions in Wardle and McLeod (1952) were of great help in identification of many of the cestode species.

In the parasite list, new locality records within the state, as well as first reports for the state, are indicated by an asterisk after the locality in question.

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List of Parasites According to Hosts

MARSUPIALIA

Didelphis virginiana, Virginia Opossum.—*Mesocestoides latus* Mueller, 1927.

INSECTIVORA

Sorex palustris, Northern Water Shrew.—*Hymenolepis parvissima* Voge, 1953; *H. parva* Rausch and Kuns, 1950.

S. ornatus, Ornate Shrew.—*Hymenolepis parva* Rausch and Kuns, 1950; *H. parvissima* Voge, 1953.

S. pacificus, Pacific Shrew.—*Hymenolepis parva* Rausch and Kuns, 1950; *Liga soricis* Neyland, 1953.

S. bendirei, Pacific Water Shrew.—*Hymenolepis parvissima* Voge, 1953.

S. vagrans, Vagrant Shrew.—*Hymenolepis parva* Rausch and Kuns, 1950.

S. sp.—*Hymenolepis sphenomorphus* Locker and Rausch, 1952; *H. parva* Rausch and Kuns, 1950.

S. trowbridgei, Trowbridge Shrew.—*Hymenolepis parva* Rausch and Kuns, 1950; *H. parvissima* Voge, 1953.

RODENTIA

Citellus beecheyi, California Ground Squirrel.—*Hymenolepis citelli* (McLeod, 1933); Larva of *Taenia* sp.; *Cysticercus portolae* Wellman and Wherry, 1910.

C. nelsoni, San Joaquin Antelope Squirrel.—*Hymenolepis citelli* (McLeod, 1933).

C. leucurus, Whitetail Antelope Squirrel.—*Oöchoristica deserti* Millemann, 1953; *Catenotaenia* sp.

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[1] Received for publication March 26, 1954.

Dipodomys heermanni, Heermann Kangaroo Rat.—*Catenotaenia linsdalei* McIntosh, 1941.

D. venustus, Santa Cruz Kangaroo Rat.—*Catenotaenia linsdalei* McIntosh, 1941.

D. panamintinus, Panamint Kangaroo Rat.—*Catenotaenia linsdalei* McIntosh, 1941; *C. californica* Dowell, 1953.

D. merriami, Merriam Kangaroo Rat.—*Catenotaenia linsdalei* McIntosh, 1941; *Oöchoristica deserti* Millemann, 1953.

D. mohavensis, Mohave Kangaroo Rat. *Catenotaenia californica* Dowell, 1953.

D. morroensis, Morro Bay Kangaroo Rat.—*Catenotaenia californica* Dowell, 1953.

Perognathus californicus, California Pocket Mouse.—*Catenotaenia linsdalei* McIntosh, 1941; *Hymenolepis horrida* (von Linstow, 1901).

P. parvus, Great Basin Pocket Mouse.—*Catenotaenia linsdalei* McIntosh, 1941.

Thomomys bottae, Valley Pocket Gopher.—*Catenotaenia linsdalei* McIntosh, 1941; *Hymenolepis citelli* (McLeod, 1933); *H.* sp.

Peromyscus californicus, California Mouse.—*Hymenolepis horrida* (von Linstow, 1901).

P. truei, Piñon Mouse.—*Hymenolepis horrida* (von Linstow, 1901).

P. boylei, Brush Mouse.—*Hymenolepis horrida* (von Linstow, 1901); larva of *Mesocestoides*.

P. maniculatus, Deer Mouse.—*Choanotaenia peromysci* (Erickson, 1938).

Reithrodontomys megalotis, Western Harvest Mouse.—*Hymenolepis citelli* (McLeod, 1933).

Neotoma fuscipes, Dusky-footed Woodrat.—*Andrya neotomae* Voge, 1946; *A. primordialis* Douthitt, 1915; *A.* sp.; *Raillietina* (*Paroniella*) sp.; larva of *Hydatigera lyncis* (Skinker, 1935).

Microtus californicus, California Vole.—*Andrya macrocephala* Douthitt, 1915.

Phenacomys longicaudus, Tree Phenacomys.—*Andrya* sp.

Rattus rattus, Black Rat.—*Hymenolepis diminuta* (Rudolphi, 1819).

R. norvegicus, Norway Rat.—*Hymenolepis diminuta* (Rudolphi, 1819); *H.* sp.; larva of *Hydatigera taeniaeformis* Batsch, 1786.

LAGOMORPHA

Lepus californicus, Blacktail Jackrabbit.—*Cittotaenia pectinata* Goeze, 1782; larva of *Multiceps* sp.

Sylvilagus audubonii, Desert Cottontail.—*Cittotaenia variabilis* Stiles, 1895; *Raillietina* (*Paroniella*) *retractilis* Stiles, 1925; larva of *Taenia pisiformis* Bloch, 1780.

S. bachmani, Brush Rabbit.—*Cittotaenia pectinata* Goeze, 1782; *Raillietina* (*Paroniella*) *retractilis* Stiles, 1925.

S. idahoensis, Pigmy Rabbit.—*Raillietina* (*Paroniella*) *retractilis Stiles*, 1925.

Ochotona princeps, Pika.—*Schizorchis ochotonae* Hansen, 1948.

CHIROPTERA

Antrozous pallidus, Pallid Bat.—*Oöchoristica* sp.

Myotis yumanensis, Yuma Myotis.—*Hymenolepis* sp.

CARNIVORA

Mustela frenata, Longtail Weasel.—*Taenia tenuicollis* Rudolphi, 1819.

Spilogale gracilis, Spotted Skunk.—*Oöchoristica pedunculata* Chandler, 1952; *O. oklahomensis* Peery, 1939; *Mesocestoides corti* Hoeppli, 1925.

Mephitis mephitis, Striped Skunk.—*Mesocestoides corti* Hoeppli, 1925; *Oöchoristica procyonis* Chandler, 1942.

Procyon lotor, Raccoon.—*Oöchoristica procyonis* Chandler, 1942.

Urocyon cinereoargenteus, Grey Fox.—*Mesocestoides corti* Hoeppli, 1925; *Taenia laruei* Hamilton, 1940; *Hydatigera laticollis* (Rudolphi, 1819).

Urocyon littoralis, Littoral Fox.—*Mesocestoides corti* Hoeppli, 1925.

Vulpes macrotis, Kit Fox.—*Mesocestoides corti* Hoeppli, 1925; *Mesogyna hepatica* Voge, 1952; *Dipylidium caninum* (Linnaeus, 1758).

Canis latrans, Coyote.—*Mesocestoides corti* Hoeppli, 1925; *M. kirbyi* Chandler, 1944; *Hydatigera lyncis* (Skinker, 1935); *Multiceps serialis* (Gervais, 1847).

Lynx rufus, Bobcat.—*Mesocestoides corti* Hoepli, 1925; *Hydatigera lyncis* (Skinker, 1935); *H. macrocystis* Diesing, 1850; *H. laticollis* (Rudolphi, 1819).

ARTIODACTYLA

Odocoileus hemionus, Mule Deer.—*Moniezia expansa* Rudolphi, 1810; *M. benedeni* Moniez, 1879; *Thysanosoma actinioides* Diesing, 1835; *Helictometra giardi* Moniez, 1879; larva of *Taenia hydatigena* Pallas, 1766; larva of *T. ovis* Cobbold, 1860; larva of *T. omissa* Lühe, 1910; larva of *Multiceps serialis* (Gervais, 1845).

Parasite List

ANOPLOCEPHALIDAE

Andrya macrocephala [=*Paranoplocephala kirbyi* Voge, 1948].—*Microtus californicus*.—Sharp Park, San Mateo Co., and Marin Co. (Voge, 1948a).

A. neotomae.—*Neotoma fuscipes*.—Hastings Reservation, Monterey Co. (Voge, 1946) and Strawberry Canyon, Alameda Co.*

A. primordialis.—*Neotoma fuscipes*.—Los Angeles Co.*

A. sp.—*Neotoma fuscipes*.—Hastings Reservation, Monterey Co. (Linsdale and Tevis, 1951).

A. sp.—*Phenacomys longicaudus*.—One-half mi. E. Stewarts Point, Sonoma Co.*

Cittotaenia pectinata.—*Lepus californicus*.—Lake Co.,* and Los Angeles Co.* *Sylvilagus bachmani*.—Berkeley, Alameda Co.*

Cittotaenia variabilis.—*Sylvilagus audubonii*.—San Joaquin Experimental Range, Madera Co. (Herman and Jankiewicz, 1943).

Moniezia expansa.—*Odocoileus hemionus*.—Hopland Field Station, Mendocino Co. (Longhurst and Douglas, 1953) and Lake Co.*

M. benedeni.—*Odocoileus hemionus*.—Hopland Field Station, Mendocino Co. (Longhurst and Douglas, 1953).

Thysanosoma actinioides.—*Odocoileus hemionus*.—Lake Co.* Hopland Field Station, Mendocino Co. (Longhurst and Douglas, 1953) and Hastings Reservation, Monterey Co. (Linsdale and Tomich, 1953).

Schizorchis ochotonae.—*Ochotona princeps*.—Bodie, Mono Co.*

LINSTOWIIDAE

Oöchoristica deserti.—*Citellus leucurus*.—Victorville, San Bernardino Co. (Millemann, 1953); *Dipodomys merriami*.—Victorville, San Bernardino Co. (Millemann, 1953).

O. procyonis.—*Procyon lotor*.—Alameda Co.* *Mephitis mephitis*.—Grey Lodge Refuge, Butte Co.*

O. pedunculata.—*Spilogale gracilis*.—Hastings Reservation, Monterey Co.*

O. oklahomensis.—*Spilogale gracilis*.—Los Angeles Co.*

O. sp.—*Antrozous pallidus*.—San Luis Obispo Co.*

CATENOTAENIIDAE

Catenotaenia linsdalei.—*Thomomys bottae*.—Hastings Reservation, Monterey Co. (McIntosh, 1941) and Berkeley, Alameda Co.;* *Dipodomys venustus, Perognathus californicus*.—Hastings Reservation, Monterey Co. (Voge, 1948b); *Dipodomys heermanni*.—San Joaquin Experimental Range, Madera Co. (Voge, 1948b); *D. panamintinus, D. merriami*. Victorville, San Bernardino Co.;* *Perognathus parvus*.—Jackass Springs, Inyo Co.*

C. californica (=*linsdalei?*).—*Dipodomys panamintinus, D. mohavensis*.—San Bernardino Co. (Dowell, 1953); *D. morroensis*.—Morro Bay (Dowell, 1953).

C. sp.—*Citellus leucurus*.—San Bernardino Co.*

MESOCESTOIDIDAE

Mesocestoides corti [*Mesocestoides variabilis* Mueller, 1927; *Mesocestoides manteri* Chandler, 1942]; (Voge, 1955).—*Urocyon cinereoargenteus*.—Mendocino Co. (Mueller, 1927), Los Angeles Co.* and Hastings Reservation, Monterey Co. (Voge, 1953a); *U. littoralis*.—Santa Rosa Island (Voge, 1953a); *Vulpes macrotis*.—Pinto Basin, Riverside Co. (Voge, 1953a); *Canis latrans*.—Hastings Reservation, Monterey Co. (Voge, 1953a); *Lynx rufus*.—Hastings Reservation, Monterey Co. (Voge, 1953a); *Mephitis*

* Indicates new record for California.

mephitis. Mendocino County, (Mueller, 1927) and Greylodge Refuge, Butte Co.;* *Spilogale gracilis*. Mendocino Co. (Mueller, 1927).

M. kirbyi.—*Canis latrans*.—Hastings Reservation, Monterey Co. (Chandler, 1944).

M. latus.—*Didelphis virginiana*.—Berkeley, Alameda Co. (Voge, 1955).

Mesogyna hepatica.—*Vulpes macrotis*.—Pinto Basin, Riverside Co. (Voge, 1952b).

Larva of *Mesocestoides* sp.—*Peromyscus boylei*.—Miguel Meadow, Yosemite National Park, (Webster, 1949).

HYMENOLEPIDIDAE

Hymenolepis parva.—*Sorex pacificus*.—Twelve mi. S. Korbel, Humboldt Co.;* *S. palustris*.—Red's Meadow, Madera Co.;* *S.* sp.—Red's Meadow, Madera Co.;* *S. vagrans*.—Skyline Boulevard, San Mateo Co.;* *S. ornatus*.—Clear Lake Park, Lake Co.;* *S. trowbridgei*.—Point Arena, Mendocino Co.*

H. parvissima.—*Sorex bendirei*.—Seven mi. E. Bayside, Humboldt Co. (Voge, 1953b); *S. palustris*.—Red's Meadow, Madera Co.;* *S. ornatus*.—Clear Lake Park, Lake Co.;* *S. trowbridgei*.—Point Arena, Mendocino Co.*

H. sphenomorphus.—*Sorex* sp.—Red's Meadow, Madera Co.*

H. citelli.—*Citellus beecheyi*.—Hastings Reservation, Monterey Co. (Linsdale, 1946) and Berkeley, Alameda Co.;* *C. nelsoni*.—Panoche Pass, San Benito Co. (Voge, 1952a); *Reithrodontomys megalotis*.—Alameda Co.;* *Thomomys bottae*.—Hastings Reservation, Monterey Co.*

H. horrida.—*Perognathus californicus, Peromyscus truei, P. boylei*.—Hastings Reservation, Monterey Co. (Voge, 1952a); *P. californicus*.—Hastings Reservation, Monterey Co. and Swanton, Santa Cruz Co. (Voge, 1952a).

H. diminuta.—*Rattus norvegicus*.—San Mateo Co., and Oakland, Alameda Co. (Voge, 1952a).

H. sp.—*Thomomys bottae*.—Berkeley, Alameda Co.*

H. sp.—*Myotis yumanensis*.—Eldorado Co.*

H. sp.—*Rattus norvegicus*.—Oakland, Alameda Co.*

DAVAINEIDAE

Raillietina (*Paroniella*) *retractilis*.—*Sylvilagus audubonii*.—San Joaquin Experimental Range, Madera County, (Herman and Jankiewicz, 1943); *S. bachmani*.—Berkeley, Alameda Co.;* *S. idahoensis*.—Mono Co.*

R. (*Paroniella*) sp.—*Neotoma fuscipes*.—Hastings Reservation, Monterey Co. (Linsdale and Tevis, 1951) and Clearlake Park, Lake Co.*

DILEPIDIDAE

Dipylidium caninum.—*Vulpes macrotis*.—Pinto Basin, Riverside Co.*

Choanotaenia peromysci.—*Peromyscus maniculatus*.—Alameda Co.*

Liga soricis.—*Sorex pacificus*.—One mile S. of Bayside, Humboldt Co.*

TAENIIDAE

Taenia tenuicollis.—*Mustela frenata*.—Alameda Co.*

T. laruei (scolices only).—*Urocyon cinereoargenteus*.—Grey Lodge Refuge, Butte Co.*

Hydatigera lyncis.—*Canis latrans*.—Hastings Reservation, Monterey Co.;* *Lynx rufus*.—Marin Co.* and California (Skinker, 1935).

H. macrocystis.—*Lynx rufus*.—Marin Co.*

H. laticollis.—*Urocyon cinereoargenteus*.—Marin Co.;* *Lynx rufus*.—California (Skinker, 1935).

Multiceps serialis.—*Canis latrans*.—Hastings Reservation, Monterey Co.*

Larva of *Multiceps serialis*.—*Odocoileus hemionus*.—Hastings Reservation, Monterey Co. (Linsdale and Tomich, 1953).

Larva of *Multiceps* sp.—*Lepus californicus*.—Lake Co.*

Larva of *Taenia ovis*.—*Odocoileus hemionus*.—Hopland Field Station, Mendocino Co. (Longhurst and Douglas, 1953).

Larva of *Taenia hydatigena*.—*Odocoileus hemionus*.—Hopland Field Station, Mendocino Co. (Longhurst and Douglas, 1953) and Hastings Reservation, Monterey Co. (Linsdale and Tomich, 1953).

Larva of *Taenia omissa.*—*Odocoileus hemionus.*—Hastings Reservation, Monterey Co. (Linsdale and Tomich, 1953).

Larva of *Taenia pisiformis.*—*Sylvilagus audubonii.*—San Joaquin Experimental Range, Madera Co. (Herman and Jankiewicz, 1943).

Larva of *Taenia* sp.—*Citellus beecheyi.*—Hastings Reservation, Monterey Co. (Linsdale, 1946).

Larva of *Hydatigera lyncis.*—*Neotoma fuscipes.*—Hastings Reservation, Monterey Co. (Linsdale and Tevis, 1951).

Larva of *Hydatigera taeniaeformis.*—*Rattus norvegicus.*—Oakland, Alameda Co.* and San Francisco (McCoy, 1909).

Cysticercus portolae.—*Citellus beecheyi.*—California (Wellman and Wherry, 1910) and Hastings Reservation, Monterey Co. (Linsdale, 1946).

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Preliminary Aerial Survey of Microbiota in the Vicinity of Davenport, Iowa

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Although considerable work has been done on that phase of aerobiology which concerns spore and pollen distribution in the atmosphere, emphasis has usually been on forms important in plant pathology or in allergy studies. Most collections have been made during long distance flights by airlines or army planes; and few papers have reported in detail on meteorological data. This paper presents six surveys of microbiota recovered by plane, at specific altitudes, from a vertical column of air; and it incorporates with the results a record of weather conditions during the flight combined with meteorological data obtained through the cooperation of the United States Weather Station located at Moline, Illinois.

Acknowledgments.—The authors are indebted to the personnel at the United States Weather Bureau Station at Moline, Illinois, for meteorological data and for helpful suggestions during the progress of this work. The authors wish to express their appreciation to Dr. J. C. Gilman, Botany Department, Iowa State College, for his assistance in the identification of certain doubtful fungus spores. The authors also wish to thank Dr. Jeannette Dean-Throckmorton of the Iowa State Medical Library, for her aid in locating references, and Dr. G. W. Martin, Botany Department, University of Iowa, for his critical reading of the manuscript.

History

It was less than one hundred years ago that scientists first began aerobiological research. Pioneer in aerobiology of the upper air was Pasteur who, with his colleagues, opened sterile flasks in the Alps in 1860. A few years later Blackley (1873), using kites, attempted to investigate the pollen content of the air above Manchester, England. Other early workers, Pouchet (1860), Maddox (1870), and Miquel (1883), studied the microbiology of the air by collecting at the tops of towers and other buildings.

For many years atmospheric research was confined to an examination of gravity slides made at or near ground level. But in 1921 Stakman and his associates (1923) began a series of studies on the incidence of fungus spores in the upper air. For the first time an airplane was used in such an investigation. Spores and pollen grains were found in relative abundance up to 11,000 feet; the highest altitude at which microorganisms were recovered was 16,500 feet. Several spores were identified; the presence of pollen grains was noted.

Pioneer in the use of the airplane to study the pollen content of the upper air was Scheppegrell (1924), who reported on the occurrence of pollen at altitudes up to 15,000 feet above the delta regions near New Orleans,

Louisiana. Other early reports of the use of the airplane for aerobiological research include: the work of Mischustin (1926) on the microorganisms found at various altitudes above Moscow, Russia; the studies on cereal rusts and other fungus spores by Craigie and Popp (1928) from southern Canada; and the observations of Weston (1929), who reported on the atmospheric flora in England. Aerobiological studies were also reported by Brown (1930), from southwestern United States; by Cotter (1931), of the United States Department of Agriculture; by Peturson (1931), of Canada; and by Hubert (1932), in Germany. In India, Chatterjee (1931) and Mehta (1933) conducted atmospheric research on cereal rust spores by using balloons.

Durham's extensive work on pollen distribution and its relation to allergy is beyond the scope of this paper. However, it should be noted that, beginning in 1931, with the cooperation of the army and airlines, Durham (1941) was able to supplement his long term investigation of gravity slides of hay fever pollen by a series of slides exposed at various altitudes up to 12,000 feet.

Few collections have been made at altitudes above 12,000 feet. Meier, Stevenson, and Charles (1933) reported the recovery of viable fungus spores at 18,000 feet. Walker (1935) reported negative results at 19,000 to 28,000 feet. Proctor (1934, 1935) recovered viable bacteria and mold spores at altitudes up to and above 20,000 feet over Boston, Massachusetts. As a result of these studies, Proctor and Parker (1938) developed an electrically controlled, automatic, sampling device which photographically recorded time, temperature, altitude, and rate of air flow while samples were being taken. Forty flights were made using this new, improved equipment. Stratosphere collections, made above 36,000 feet with a balloon-borne sampling device, which was controlled by an aneroid barometer, were reported by Rogers and Meier (1936 a, b). Several genera of Fungi Imperfecti were obtained.

The probable importance of air currents in the dissemination of microorganisms had been recognized for some time. However, aerial collections had always been made in latitudes where the close proximity of vegetation offered a possible local source of spores and pollen. Concrete evidence that air currents are a significant factor in the distribution of microorganisms over a long distance was established by Lindberg in 1933 (Meier and Lindberg, 1935) when he exposed petroleum-covered slides while flying in the Arctic Circle over the North Atlantic. Fifty-nine different kinds of objects, most of them organic in origin, were recovered from the air over ice and water. Other collections made from marine air were described by Bisby (1935), Meier (1936), Erdtman (1938), Rittenberg (1939), and Newman (1948).

During the twelve years between 1935 and 1947 relatively few papers appeared on the subject of aerobiological collections made by airplane. The recovery of fungus spores, bacteria, and pollen grains from the air over Omaha, Nebraska, was reported by MacQuiddy (1935). Van Overeem (1936) described a new sampling apparatus, consisting of glass-wool packed tubes, with which he recovered not only fungi and bacteria, but also algae and moss protonema. Meier and Artschwager (1938), while making airplane collections of sugar beet pollen, recovered pollen from other species of plants; fungus spores; and plant hairs. In the same year Tasugi and Kurosawa (1938) called attention to the fact that the angle of attack between the

collecting device and the air stream affects the number of fungus spores recovered; more spores were caught when slides or petri dishes were held at right angles. Craigie (1939) reviewed the literature on aerial dissemination of plant pathogens. In 1942 the American Association for the Advancement of Science published a symposium (1942) which summarized the status of aerobiological knowledge at that time. Wolf (1943) reported on six flights made between October and February over Nashville, Tennessee. Petri dish collections were made at various altitudes up to 10,000 feet, and the numbers of bacterial and fungal colonies as well as identification of the isolates was given. Weather records as to temperature, relative humidity, wind direction, and velocity were tabulated, but no correlation attempted.

Recent papers on aerobiological research in the upper atmosphere include the work of Heise and Heise (1948, 1949), who in 1948 gave a quantitative report on the nocturnal and diurnal variation in number of ragweed pollen and *Alternaria* spores found at various altitudes near Milwaukee, Wisconsin, and in 1949 described the influence of temperature and wind variations on the distribution of ragweed pollen and *Alternaria* and rust spores. Sack (1949) reported on long distance dissemination of pollen grains; data collected by ships in transatlantic crossings were supplemented by airplane collections made on a flight from New York to Bermuda.

Extensive aerobiological research was begun in Canada in 1947. Polunin, Pady, and Kelly (1947) reported briefly on the numbers of bacteria and fungi recovered from arctic air. Subsequent reports analyzed the 1947 collections. Bacteria were found to outnumber fungus spores in the arctic air, according to Pady, Kelly, and Polunin (1948). The presence of cereal pathogens was noted, and associated cereal diseases reviewed by Pady, Peturson, and Green (1950). Identification of saprophytic soil forms presumably carried north by air currents was described in some detail by Pady (1951); attention was called to the desirability of meteorological data as an aid to the interpretation of results. In 1949 and 1950, through the cooperation of the Royal Canadian Air Force, techniques and equipment were developed for extensive air sampling. Pady and Kelly (1949) and Kelly, Pady, and Polunin (1951) described this equipment. Subsequently, collecting flights were made over both arctic and non-arctic regions. During ten flights over non-arctic regions of Canada three different methods of collecting bacteria and fungus spores were used. Kelly and Pady (1953) compared the relative values of the sampling methods used and reported on the numbers of organisms obtained. Meteorological data were correlated with the collections in an attempt to determine the source of the organisms. Pady and Kelly (1953) also reported on the numbers of fungi and bacteria recovered during three flights over arctic regions and compared the results with collections made at ground level.

MATERIALS AND METHODS

The area surveyed, as established by reference points on the ground, was a column of air ten miles in diameter and 5000 feet high over farm lands northeast of the city of Davenport, Iowa. An Aeronca Chief airplane was used; R.P.M. was 2150; airspeed was 85 miles per hour. Collections were made for two minutes' duration every 500 feet during a descent from 5000 feet altitude. The first exposure was made at the maximum altitude because

it was felt that exposure of the plane to the airstream during the climb decreased the possibility of contamination from the plane surface.

Seven trial flights were made in order to perfect techniques. Then six collecting flights were made, one every four to six days, for a thirty-three day period. With one exception, due to weather interference, the time of collection was always the same: namely, between 1:30 and 3:30 P.M. Early summer, June 12 to July 14, 1951, was the time chosen, so as to post-date local tree pollination and pre-date ragweed pollination, thus facilitating the checking of other biological objects. Quantitative counts were made and, whenever possible, biological objects were identified. No cultural studies were attempted.

Meteorological data recorded at the time of collection included 1) cloud type, 2) cloud base altitude, 3) percent overcast, 4) temperature at each altitude, 5) relative humidity at ground level, 6) precipitation in last twenty-four hours, 7) visibility, 8) wind direction, 9) wind velocity, and, 10) when the information was available, winds aloft at 2,000, 4,000, and 6,000 feet altitude. In addition to this information, the official daily United States Weather Maps were procured for the months of June and July.

The collecting device used was designed by the senior author. The apparatus consisted of a metal frame made of two parallel channels facing each other to form a track to carry a sliding cartridge perpendicular to the air stream. The device was clamped to the window frame of the plane and extended outward ten inches. The cartridge was a block of wood hollowed out to hold a 1 x 3 inch glass slide, and was grooved for a sliding metal cover. The movement of the cartridge along the track and the opening and closing of the cover were accomplished by means of wires manipulated from inside the plane.

The collecting slides were prepared as described by Wodehouse (1935). The collecting medium used was glycerine jelly, to which had been added methyl green as a stain. The colored glycerine jelly was melted and applied to each side as two 18 mm discs, by using a camel's hair brush as the applicator while the slide was manipulated on a turn-table. Immediately upon completion of the preparation a slide was put into its cartridge. Cartridges were always loaded in still air in a closed room, using bacteriological precautions. Following exposure, the cartridges were returned to the laboratory, where they were opened and the slides removed. Each glycerine disc was then covered with an 18 mm cover slip. After microscopic examination, each mount was ringed with black lacquer for storage. Before reloading, the cartridges were blown out with compressed air to avoid the possibility of contamination from previous exposures. Control cartridges carried during all observations consistently gave negative results.

For comparative purposes, gravity slides of twenty-four hours' duration were made, starting at 5 P.M. on the day preceding the airplane collection. The collecting apparatus used was located at the airport, and was built to meet the specifications of the National Pollen Survey Committee of the American Academy of Allergy (1946).

RESULTS

The collections made on the six different days represent a total of sixty-five exposures, of which sixty were on altitude slides; the remaining five were

on gravity slides. The sixth gravity slide was lost, due to adverse weather conditions. Objects of both botanical and zoological origin were recovered; most numerous were those of botanical origin.

The most conspicuous objects recovered were the pollen grains, which totaled 1345. Of this total, 1294 were identified. The degree to which identification was possible varied greatly. In some cases, identification as far as species was possible; in other cases, identification was made to family only. Wodehouse (1935) and Brown (1949) were used as authorities.

Distribution of identified pollen grains varied. Eight kinds of pollen grains were common to both altitude and gravity slides. Arranged in order of frequency of occurrence these were: Gramineae (986); Urticaceae, other than *Morus* and *Maclura,* (82); *Pinus* (51); *Plantago lanceolata* (35); Chenopodiaceae, indistinguishable from the related family Amaranthaceae, (24); *Morus alba* (10); *Maclura pomifera* (9); and *Juglans* (5). Nine kinds of pollen were found on altitude slides only. These included: *Polygonum* (38); *Ambrosia* (18); *Typha latifolia* (12); *Ginko* (6); *Ephedra* (5); *Cycas* (4); Cyperaceae (4); *Juglans cinerea* (3); and Polygonaceae, other than *Polygonum* (2). No pollen grains were confined to gravity slides alone. The total yield from gravity slides was 200 pollen grains, of which 198 were identified. A total of 51 pollen grains was unidentified; these represent 10 different kinds. Except for 2 on the gravity slide of July 7, all other unidentified pollen grains were confined to altitude slides.

Because the identification of fungus spores usually depends upon the presence of the mycelium from which they originated, recognition is difficult, and often impossible, without cultural studies. The total number of fungus spores was 2323, of which 1448 were identified. In order of frequency of occurrence these were: *Cladosporium,* sometimes known as *Hormodendrum,* (844); *Alternaria* (364); *Phyllachora trifolii* (170); and *Stemphylium* (68). Two *Fusarium* spores were found on a gravity slide; all other identified spores were common to both gravity and altitude slides. *Helminthosporium* was conspicuous by its absence. With one exception the unidentified spores were found on both altitude and gravity slides. In an attempt to determine the amount of variability among the 875 unidentified spores, an arbitrary, artificial classification based on common morphological differences was established. Factors considered were shape, color, size, and segmentation. A surprising degree of uniformity was encountered in the spores recovered. It was practical to subdivide the unidentified forms into seven categories as follows. The number of spores of each kind is indicated in parentheses.

Spherical, hyaline (318)—Average size 11μ (284); others .....(34)
Spherical, green (470)—Average size 6μ (388); others .....(82)
Spherical, brown (39)—Average size 24μ (24); others .....(15)
Spherical, black—Average size 38μ .....(6)
Ovoid, hyaline—Average size 17 x 20μ .....(12)
Ovoid, brown—Average size 8 x 17μ .....(7)
Segmented (23)—Hyaline, 5-celled, 9 x 32μ (16); others .....(7)

Miscellaneous objects of botanical interest included a broken fern sporangium, a fragment of *Sphagnum* thallus, trichomes of the branched, multicellular type, and xylem fragments; some of the latter showed annular thickenings, others showed spiral thickenings, and several showed bordered pits.

TABLE 1.—Survey and weather data, June 12, 1951

	Gravity	Altitude in feet 500	1000	1500	2000	2500	3000	3500	4000	4500	5000
	Temperature °F										
	67	68	68	67	65	63	61	60	58	55	54
POLLEN GRAINS											
Gramineae	10	1	....	....	2	5	8	10	2	10	14
Ginko	....	....	....	....	....	....	....	....	....	2	1
Morus alba	....	....	1	....	....	....	....	....	....	3	....
Maclura pomifera	2	....	....	1	1	....	....	....	....	....	....
Polygonum	....	....	....	....	....	....	....	....	....	1	....
Ambrosia	....	....	....	....	....	....	....	1	1	1	....
Other	....	....	....	....	....	....	1	....	....	....	....
FUNGUS SPORES											
Alternaria	10	....	....	....	....	2	3	....	....	2	1
Cladosporium	24	2	2	....	....	2	1	1	....	2	14
Phyllachora trifolii	2	....	....	....	....	....	....	....	3	....	....
Spherical hyaline	....	....	....	....	....	1	....	....	....	4	....
Spherical, brown	1	....	....	....	....	....	....	1	....	....	....
Ovoid browns	1	....	....	....	....	1	....	....	....	....	....
NEMATODE EGGS	....	....	....	....	....	....	1	2	1	2	3
OTHER OBJECTS											
Trichome	x	....	....	....	....	....	....	....	....	....	....
Fern sporangium	....	....	....	....	....	....	....	x	....	....	....

Cloud type	Cumulus	Wind direction	
Overcast	5/10	Velocity	calm
Cloud base	2200	Winds at 2000	120/10
Visibility	15	Winds at 4000	90/6
Humidity	82	Winds at 6000	
Precipitation	0.45	Time of day	6:18-6:48 P.M.

Remarks: Top of clouds 5000; intermittent thundershowers; collection made immediately after a thundershower.

Zoological objects which were recovered included a butterfly scale, insect antennae of the filiform type, a mite, 3 nematodes, and 323 objects which are presumably nematode eggs. It is interesting to note that these last were recovered at every altitude.

Tables 1-6 show the distribution by altitude of the various objects recovered and the weather data recorded at the time of collection. Terms used in tabulating the weather data may be interpreted as follows:

Altitude: All altitudes are the measured distance above the ground, using the Davenport Air Park at 690 feet above sea level as the base point.

Cloud type: Self-explanatory.

Overcast: Fraction of the sky covered by clouds, expressed in tenths; i.e., 1/10—very scattered clouds; 10/10—sky obscured.

Cloud base: The measured distance from the ground to the lowest part of the cloud, expressed in feet.

Visibility: The distance toward the horizon at which prominent objects can be seen and identified, expressed in miles.

Humidity: Relative humidity at ground level, expressed in percent.

Precipitation: Amount of precipitation in the last twenty-four hours, expressed in inches.

Wind direction: Direction from which the wind is blowing.

Velocity: Expressed in miles per hour at ground level.

Winds at 2000, 4000, 6000: Wind direction and velocity aloft at respective altitudes, expressed by two numbers, the first being compass direction, the second being the velocity in knots; i.e.., 90/6—wind is blowing from the east at a velocity of 6 knots (knot —6080.2 feet per hour).

Figures 1-6 show correlations between total spore and total pollen counts and altitude. The cloud base, when under 5000 feet, is represented by a broken vertical line. Due to the wide range in counts it was found practical to use a three cycle semi-logarithmic plot with a zero base line added.

DISCUSSION

Table 1 and fig. 1 indicate an increase in the number of biological objects with an increase in altitude. This is contrary to the anticipated curve which would be expected to show a decrease in number with an increase in altitude.

TABLE 2.—Survey and weather data, June 16, 1951

	Altitude in feet										
	Gravity	500	1000	1500	2000	2500	3000	3500	4000	4500	5000
	Temperature °F										
	78	74	71	70	68	66	64	62	60	60	58
POLLEN GRAINS											
Gramineae	79	22	19	15	31	2	2	....	3	1	2
Morus alba	1	1	1	1	....	....	....	....	....	....	....
Maclura pomifera	....	....	....	....	1	....	....	....	....	....	....
Other Urticaceae	....	....	3	....	....	....	....	....	....	....	....
Polygonum	....	....	1	....	....	....	....	....	....	....	....
Pinus	....	....	1	1	....	1	....	....	....	....	....
Typha latifolia	....	4	....	....	....	....	....	....	....	....	....
Other pollen	....	....	....	....	....	1	1	....	....	....	1
FUNGUS SPORES											
Alternaria	9	7	1	2	13	....	....	....	....	2	....
Cladosporium	130	9	....	15	16	....	....	....	....	1	....
Phyllachora trifolii	8	....	4	....	1	....	....	....	....	....	....
Stemphylium	2	....	1	....	2	....	....	....	....	....	....
Fusarium	2	....	....	....	....	....	....	....	....	....	....
Spherical, hyaline	27	....	....	1	10	....	1	....	1	1	....
Spherical, green	2	....	48	7	5	....	1	....	....	....	....
Spherical, brown	....	1	....	....	2	....	....	....	....	....	....
Spherical, black	2	....	....	....	....	....	....	....	....	....	....
Ovoid, brown	1	....	....	1	....	....	....	....	....	....	....
Segmented	3	....	....	4	1	....	....	....	....	....	....
NEMATODE EGGS	1	....	....	....	....	....	....	....	....	....	....
OTHER OBJECTS											
Trichomes	x	x	x	....	....	....	....	....	....	....	....
Sphagnum fragment	x	....	....	....	....	....	....	....	....	....	....

Cloud type	Cumulus	Wind direction	SE
Overcast	7/10	Velocity	12
Cloud base	2200	Winds at 2000	150/12
Visibility	10	Winds at 4000	clouds
Humidity	67	Winds at 6000	clouds
Precipitation	0.01	Time of day	2:41-3:10 P.M.

Remarks: Top of clouds 4500; turbulent up to 2000.

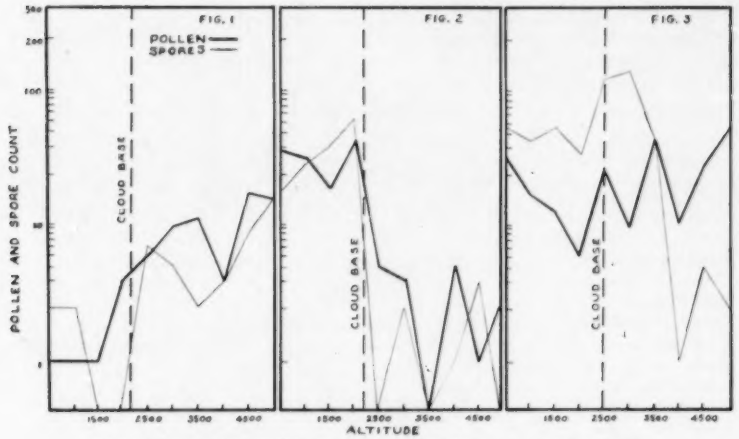
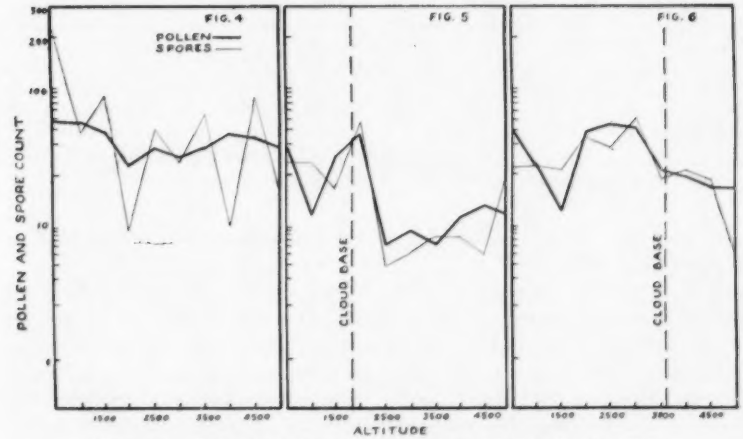


FIG. 1-3.—Pollen and Spore Curves for June 12, 16, 23, 1951.

However, this collection was made after repeated thunder showers; it is presumed that the rain washed the objects from the air below the cloud level. This agrees with Meier's (1936) report that there is a reduction in microorganisms below the cloud level following precipitation.

Table 2 and fig. 2 show what is assumed to be a characteristic curve with an abrupt diminution in numbers of objects above the cloud base. This corroborates Scheppegrell's (1924) opinion that the bulk of the pollen load will usually be below the altitude of cloud formation. The completely blank slide at 3500 feet is not to be considered remarkable if the paucity of grains at the higher altitudes is taken into account. The turbulence encountered up to 2000 feet further explains the higher numbers of objects found at the



FIGS 4-6.—Pollen and Spore Curves for June 30, July 7, 14, 1951

TABLE 3.—Survey and weather data, June 23, 1951

	Gravity	Altitude in feet 500	1000	1500	2000	2500	3000	3500	4000	4500	5000
	Temperature °F										
	72	70	67	65	63	61	60	62	62	62	63
POLLEN GRAINS											
Gramineae	31	21	7	8	4	18	2	31	8	14	25
Ginko	....	....	....	....	....	....	....	3	....	....	....
Maclura pomifera	....	....	1	....	....	....	....	....	....	....	1
Other Urticaceae	....	3	....	....	....	....	....	....	....	....	....
Polygonum	....	....	3	....	....	....	....	....	....	....	....
Other Polygonaceae	....	....	....	....	....	....	2	....	....	....	....
Ambrosia	....	....	....	....	1	....	....	....	....	....	....
Pinus	....	1	1	1	....	....	....	....	....	7	7
Chenopodiaceae	....	....	....	....	....	....	....	....	....	1	2
Plantago lanceolata	1	....	....	2	....	1	1	....	1	....	1
Ephedra	....	....	....	....	....	....	....	....	....	1	4
Juglans cinerea	....	....	....	....	....	2	....	....	....	....	....
Other	....	....	1	....	....	....	3	3	....	....	....
FUNGUS SPORES											
Alternaria	9	1	7	7	4	11	7	1	....	4	2
Cladosporium	252	13	....	15	1	59	65	3	....	....	1
Phyllachora trifolii	14	5	1	....	1	....	11	....	....	....	....
Stemphylium	1	2	1	4	....	4	....	....	1	....	....
Spherical hyaline	11	21	24	14	14	28	17	30	....	....	....
Spherical, green	....	1	....	....	1	1	25	....	....	....	....
Spherical, black	4	....	....	....	....	....	....	....	....	....	....
Ovoid, brown	....	....	....	....	3	....	....	....	....	....	....
Segmented	1	1	....	....	1	....	1	....	....	....	....
NEMATODE EGGS	....	....	1	....	1	5	....	....	....	....	....
OTHER OBJECTS											
Trichomes	x	....	....	....	....	....	....	x	....	....	....
Insect antennae	....	....	x	....	....	....	....	....	....	....	....
Nematode	....	....	....	....	....	x	....	....	....	....	....
Butterfly scale	x	....	....	....	....	....	....	....	....	....	....

Cloud type	Fractostratus	Wind direction	SE
Overcast	10/10	Velocity	7
Cloud base	2500	Winds at 2000	150/8
Visibility	8	Winds at 4000	clouds
Humidity	64	Winds at 6000	clouds
Precipitation	0	Time of day	2:22-2:52 P.M.

Remarks: Top of first cloud level 3000; hazy below first cloud level; solid overcast above 5000. Note inversion of temperature.

lower altitudes. Heise and Heise (1949) encountered this same situation in regard to turbulence.

Table 3 and fig. 3 indicate an increase in number of objects above the cloud base. This again is contrary to expectation. However, in this case a temperature inversion (i.e., an increase in temperature with an increase in altitude) would seem to indicate that the warm air mass encountered above the cloud was not of local origin. This inference appears to be justified by the recovery of *Ephedra* and pine pollen grains at the higher altitudes. The date of this collection precludes the probability of local origin for the pine pollen, and,

as far as is known, there is no local source for *Ephedra*. Long distance traveling of pollen cannot be considered unusual in view of the report of Meier and Lindberg (1935) on the recovery of microorganisms from the air over the Atlantic and the report of Pady and Kelly (1953) on the collection of fungus spores and bacteria from the arctic air over Canada.

Table 4 and fig. 4 show a very striking spore count curve. This is to be expected inasmuch as many strong updrafts were encountered which would carry large quantities of material to the upper altitudes. It was on this day that the altitude slides showed the highest number of biological objects. No explanation is offered for the fact that the pollen curve does not follow the

TABLE 4.—Survey and weather data, June 30, 1951

	Altitude in feet										
	Gravity	500	1000	1500	2000	2500	3000	3500	4000	4500	5000
	Temperature °F										
	74	70	68	66	62	60	58	56	52	51	50
POLLEN GRAINS											
Gramineae	*	35	30	27	10	17	12	18	19	19	18
Urticaceae	....	5	8	4	2	4	6	2	5	2	2
Polygonum	....	1	....	....	3	....	....	....	1	4	2
Ambrosia	....	2	2	1	....	....	....	....	....	....	....
Pinus	....	....	....	....	2	....	....	....	....	....	....
Typha latifolia	....	....	....	....	....	....	....	4	4	....	....
Plantago lanceolata	....	....	2	1	....	1	2	....	2	....	2
Juglans cinerea	....	....	1	....	....	....	....	....	....	....	....
Cycas	....	1	....	....	1	....	....	....	....	....	....
Cyperaceae	....	1	2	1	....	....	....	....	....	....	....
Other	....	2	1	2	3	5	3	....	5	5	3
FUNGUS SPORES											
Alternaria	....	10	5	1	3	6	10	9	6	3	5
Cladosporium	....	7	4	....	....	20	....	25	....	....	5
Phyllachora trifolii	....	3	1	1	3	1	3	2	2	5	1
Stemphylium	....	2	....	....	2	....	2	1	1	2	....
Spherical hyaline	....	....	5	12	....	2	5	1	....	1	5
Spherical, green	....	200	23	60	....	....	....	....	....	60	....
Spherical, brown	....	....	....	....	1	9	....	....	....	....	....
Ovid, hyaline	....	....	....	....	....	....	....	12	....	....	....
Segmented	....	1	1	....	....	....	1	....	....	....	....
NEMATODE EGGS	....	....	....	1	3	1	6	2	....	....	....
OTHER OBJECTS											
Trichome	....	x	....	x	x	....	....	....	....	....	....
Insect antennae	....	....	....	....	....	....	....	....	x	....	....
Mite	....	....	....	....	....	....	....	....	....	x	....
Xylem fragment	....	....	x	....	....	....	....	....	....	x	....

Cloud type	Cumulus	Wind direction	W
Overcast	5/10	Velocity	15
Cloud base	5100	Winds at 2000	290/18
Visibility	Unlimited	Winds at 4000	290/17
Humidity	45	Winds at 6000	310/12
Precipitation	0.02	Time of day	2:08-2:35 P.M.

Remarks: Very turbulent; many strong updrafts.

* Gravity slide was lost.

erratic trend shown by the spore count curve. Possibly a study of the aerodynamics involved would explain this variation.

Table 5 and fig. 5 represent the most interesting collection of the series. Although fig. 5 indicates only the expected diminution above the cloud base, a reference to table 5 shows the unusual presence of pine pollen. Inasmuch as July 7, the date of this collection, postdates local pine pollination, the inference is that these pollen grains are of foreign origin. Confirmation of this is offered by a perusal of the daily weather maps for the seven days preceding this collection. The weather maps show that there was an intrusion of a continental polar air mass during this time. Subsequently pine pollen was recovered at almost every altitude, the greater number being recovered above the cloud base. Kelly and Pady (1953) call attention to the possibility of using fungus spores as evidence of air mass origins. However, the ubiquitous nature of fungus spores would seem to make them less desirable

TABLE 5.—Survey and weather data, July 7, 1951

	Altitude in feet										
	Gravity	500	1000	1500	2000	2500	3000	3500	4000	4500	5000
	Temperature °F										
	86	80	78	76	77	78	76	74	73	71	70
POLLEN GRAINS											
Gramineae	32	13	3	7	24	....	....	1	....	1	1
Morus alba	1	....	....	....	....	....	....	....	....	1	....
Other Urticaceae	3	7	2	3	6	....	....	....	....	1	3
Polygonum	....	1	2	8	2	....	2	....	....	....	....
Ambrosia	....	....	....	....	....	....	....	....	1	....	....
Pinus	....	2	2	1	....	4	3	3	7	3	3
Chenopodiaceae	1	1	....	....	3	1	3	1	2	3	3
Plantago lanceolata	1	2	3	1	1	1	....	1	....	2	....
Juglans	1	....	....	....	....	....	....	....	....	....	....
Cycas	....	....	....	....	1	....	....	....	....	1	....
Other	2	3	....	5	....	....	....	....	....	....	1
FUNGUS SPORES											
Alternaria	19	7	2	4	3	....	....	....	3	....	6
Cladosporium	17	4	1	2	31	....	2	....	....	....	1
Phyllachora trifolii	8	11	19	7	14	....	....	....	....	....	....
Stemphylium	....	....	1	....	....	....	....	....	....	....	....
Spherical, hyaline	4	1	....	....	....	3	3	....	3	6	11
Spherical, green	2	....	....	4	....	....	....	7	....	....	....
Segmented	....	....	....	....	....	1	....	....	1	....	....
NEMATODE EGGS	11	47	12	20	6	....	....	....	....	....	....
OTHER OBJECTS											
Nematode	....	....	....	....	....	....	....	....	x	....	....
Xylem fragments	....	x	....	....	....	....	....	....	x	....	x

Cloud type	Cumulus	Wind direction	S
Overcast	1/10	Velocity	15
Cloud base	1800	Winds at 2000	200/14
Visibility	7	Winds at 4000	230/18
Humidity	64	Winds at 6000	clouds
Precipitation	0	Time of day	1:38-2:07 P.M.

Remarks: Top of clouds 2700; hazy below and above clouds. Note slight inversion of temperature.

in such a capacity than pollen grains, whose time availability from local sources is usually well defined.

Table 6 and fig. 6 show an interesting, but unexplained, relatively constant pollen count persisting through a thousand foot layer from 2000 to 3000 feet altitude, followed by the normal diminution in the neighborhood of the cloud base. The weather data showed no unusual features except a sixty degree wind shift between 2000 and 4000 feet altitude.

From the data available it is interesting to note that there is not always a correlation between the kinds of organisms, especially pollen grains, found on gravity slides and those recovered on aerial slides. Except for two kinds of fungus spores, all other kinds of fungus spores and all pollen grains found on gravity slides were also found on aerial slides; but, in several cases, microbiota recovered from aerial slides were never recovered from gravity slides. It would appear that aerial slides will give a more accurate survey of the biologic content of the air than will gravity slides.

The diminution level for microorganisms has been reported for several

TABLE 6.—Survey and weather data, July 14, 1951

	Altitude in feet										
	Gravity	500	1000	1500	2000	2500	3000	3500	4000	4500	5000
	Temperature °F										
	82	78	75	72	70	67	65	62	60	59	58
POLLEN GRAINS											
Gramineae	31	35	15	12	43	48	49	17	15	15	12
Maclura pomifera	....	....	....	....	2	....	....	....	....	....	....
Other Urticaceae	....	1	2	....	....	4	2	1	....	....	1
Polygonum	....	3	....	....	2	....	....	1	1	....	....
Ambrosia	....	....	6	....	....	....	....	....	....	1	1
Pinus	1	....	....	....	....	....	....	....	....	....	....
Chenopodiaceae	1	....	....	....	....	1	....	....	....	....	1
Plantago lanceolata	1	1	....	....	....	....	1	....	2	....	1
Juglans	1	....	....	....	1	2	....	....	....	....	....
FUNGUS SPORES											
Alternaria	55	14	13	5	13	12	15	5	7	11	7
Cladosporium	66	....	....	....	2	2	25	....	2	....	....
Phyllachora trifollii	10	1	1	4	4	3	4	5	3	4	....
Stemphylium	5	4	2	4	7	3	6	3	1	3	1
Spherical, hyaline	18	1	5	4	9	4	3	....	7	....	....
Spherical, green	15	....	....	....	1	2	....	5	....	....	....
Spherical, brown	2	2	4	4	6	4	2	....	....	....	....
Segmented	2	1	....	1	1	....	....	....	....	....	1
NEMATODE EGGS	30	49	19	10	23	36	16	25	8	14	9
OTHER OBJECTS											
Nematode	....	....	x	....	....	....	....	....	....	....	....
Xylem fragment	....	x	....	....	....	....	....	....	....	....	....

Cloud type	Cumulus	Wind direction	S
Overcast	4/10	Velocity	10
Cloud base	3600	Winds at 2000	190/6
Visibility	15	Winds at 4000	250/4
Humidity	54	Winds at 6000	260/5
Precipitation	0	Time of day	2:52-3:19 P.M.

Remarks: Top of clouds 4500; hazy below the clouds.

different altitudes by different workers. According to Durham (1941), the bulk of a pollen load is below 3000 feet; Heise and Heise (1948) found the greatest concentration at 3500 feet; Sack (1949) reported a rapid fall in concentration above 4000 feet. In no case was reference made to a relation between diminution and cloud level. From the data plotted in figs. 1-6 it appears evident that, if the cloud base is below 5000 feet, diminution of concentration of biological objects is usually related to the cloud base rather than to any specific altitude.

Although Wolf (1943) was not able to find a correlation between humidity and cultural studies of fungi, an analysis of the relation between aerial counts and relative humidity at ground level (tables 1-6) indicates that the higher the relative humidity, the lower the number of biological objects recovered from the air. Prolonged precipitation may be followed by diminution of biological objects below a cloud base, but not necessarily above it.

No correlation was found between temperature and count of microorganisms recovered, except that an unusual change in temperature, such as an inversion, may indicate the presence of a different air mass, which could have an entirely different biological content. While a high rate of temperature fall or lapse rate, as reported by Heise and Heise (1949), often denotes turbulent air, this can by no means be considered universally true for all localities, inasmuch as table 6 and fig. 6 show a relatively high lapse rate, but no unusual turbulence was noted.

It is probable that departures from the norms can be explained by analysis of meteorological data. However, while the accumulated records of such meteorological factors as overcast, cloud type, visibility, wind direction, velocity, and winds aloft seem to indicate certain trends, it was felt that the data was too meager to draw any definite conclusions therefrom. It is obvious that only a long term study of daily collections and daily weather records could give a true picture of the relation between weather factors and the aerial distribution of biological objects.

SUMMARY

Aerial collections were made by airplane at 500 foot intervals up to 5000 feet altitude. Gravity slides supplemented these collections.

The most conspicuous objects recovered were pollen grains. Seventeen different kinds were identified, of which nine different kinds were confined to altitude slides.

The most numerous objects recovered were fungus spores. Of the 2323 spores recovered, 1442 were identified as *Cladosporium, Alternaria, Phyllachora trifolii, Stemphylium,* and *Fusarium.* All but one kind of spores were found both on altitude and gravity slides.

Miscellaneous botanical objects included a fern sporangium, a fragment of *Sphagnum,* trichomes, and xylem fragments.

Zoological objects included a butterfly scale, insect antennae, a mite, nematodes, and presumably nematode eggs.

An attempt was made to correlate meteorological data with the tabulated records of collections at different altitudes.

Diminution of concentration of biological objects appears to be related to cloud base rather than to any definite altitude.

The higher the relative humidity at ground level, the lower was the number of objects recovered from the air.

Possibly the identification of pollen grains will furnish evidence as to air mass origins.

Aerial slides give a more comprehensive survey of the biologic content of the air than do gravity slides.

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Quantitative Distribution, Forest Soil Microorganisms in a Yellow Poplar Plantation[1]

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Since living microbes such as fungi, bacteria, and actinomycetes exert a profound influence upon the genetical development of soil profiles, they also exert an indirect effect upon the growth of forest trees. This is accomplished by altering the physical, chemical, and microbiological characteristics of the soil profile. Although the quantity, or numbers of organisms in any given soil, are only relative indices of forest soil fertility, these quantitative counts may offer clues as to the effect of other site factors. Lohnis and Fred (1923) came to the conclusion that a determination of bacterial numbers in the soil is worthless as an attempt in interpreting soil phenomena. However, later investigators (Waksman, 1927; Waksman and Starkey, 1931) have clearly shown that studies on the numbers of organisms are important as well as indicative, when used in conjunction with other edaphic and climatic factors. In comparing numbers of bacteria, no single variable such as season of the year can be considered alone without reference to moisture content, acidity, and other factors, as shown by Waksman (1927). Studies of soil organisms in both natural and planted forest stands by Shipman (1947) have demonstrated that forest site quality is indirectly related to soil organism populations. Soil, whether in a natural state or once in cultivation, cannot be considered uniform in its spatial distribution of soil microorganisms. While the qualitative distribution of soil organisms remains much the same, there are very marked differences in the quantitative relationships of a given soil area (Waksman and Starkey, 1931). It is important to study these numerical variations, as expressed by horizon differentiation, whether visible natural horizons are present or not. In evaluating existing forest sites for actual or potential growth, or in appraising the value of any land to produce a crop, one cannot ignore the soil inhabitants and their effect upon the final crop. This microbial effect may be direct, as in the case of soil pathogens, or it may be indirect by altering the physical and chemical characteristics of the crop substrate. A field and laboratory study was undertaken to determine the total numbers, horizonal distribution, and seasonal fluctuation of certain forest soil organisms under a combination of environmental factors.

Study Area

The experimental area, a 15-year-old 20-acre yellow poplar plantation, located in southwestern Michigan, exhibited a marked and significant difference in height growth between two portions of the same plantation. A recent experimental study in the same area had shown that the significant difference in height growth was primarily a function of the soil moisture regimen throughout

[1] Portion of a thesis submitted to the Graduate School of Michigan State College in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Forestry.

TABLE 1.—Influence of certain physical and chemical edaphic factors upon the numbers of organisms in soils of planted yellow poplar

Soil Horizon and Depth	Soil Texture Percent									Numbers of Organisms per Gram soil*		
	Fine clay	Sand	Silt plus clay	Soil pH	Soil Moisture Percent	Organic Matter Percent	Nitrogen Percent	C/N Ratio	Total Porosity Percent	Bacteria	Fungi	Actinomycetes
Area G (good height growth)												
A_0 (0- 1")	....	....	....	5.9	21.9	....	....	....	....	1,741,620	10,390	55,150
A_1 (1- 9")	13.2	61.5	38.5	5.4	15.3	2.03	.119	20:1	46.8	887,000	5,970	34,280
A_2 (9-15")	14.3	69.9	30.1	5.2	14.7	.83	.045	21:1	37.8	1,305,500	4,430	13,870
B_2 (15-23")	18.7	74.8	25.2	5.3	12.2	.68	.044	18:1	....	113,080	16,710	71,820
Area P (poor height growth)												
A_0 (0- 1")	....	....	....	5.7	20.3	....	....	....	....	1,695,640	8,810	62,120
A_1 (1- 9")	15.1	59.2	40.8	5.3	14.5	2.16	.127	19:1	48.9	2,043,750	9,630	41,370
A_2 (9-12")	18.5	62.2	37.8	5.0	16.6	1.04	.063	19:1	42.5	1,451,000	9,510	26,890
B_2 (12-22")	21.7	69.0	31.0	4.8	12.0	.79	.057	16:1	....	120,100	15,140	8,990

*Each value represents the average product of four seasonal isolations times six duplicate plates, or the average of forty-eight plates per soil horizon taken periodically throughout the growing season.

the growing season (Shipman and Rudolph, 1954). As a part of this study an opportunity was provided to investigate the quantitative soil microbial relationships under both height growth conditions. The portion of the yellow poplar plantation representative of good height growth was designated as Area G; the portion of poor height growth as Area P. Both portions of the plantation were of the same age and density, and the soils had undergone injudicious cropping without fertilization for many years prior to plantation establishment some 15 years ago. The study area is located within the Gray-Brown Podzolic soil group of southwestern Michigan and consists of an outwash plain and other sandy drift of glacial origin. The soils of Area G were mapped as acid variants of a sandy loam, while those of Area P are acid variants of a loam to sandy loam containing greater amounts of clay.

MATERIALS AND METHODS

Field Sampling.—Quantitative microbial isolations were made in each experimental area in order to determine the extent and magnitude of numerical differences of soil organisms existing within both height growth areas. At periodic intervals throughout the growing season of 1951, soil sampling was systematically carried out at four established stations, two in each portion of the forest stand. Samples were collected in glass containers of 65 milliliter capacity, previously sterilized in an oven at 105°C for one hour. Sterilized lids were then screwed tightly to the empty glass containers and taken directly into the field. By means of a post-hole digger, which was sterilized by ignition of alcohol before each excavation, soil profiles were exposed to an appropriate depth. Using an ordinary sterile, wooden ice-cream spoon, enough soil was extracted at fixed soil horizon depths to fill each container. The wooden spoon was discarded following each individual soil sampling. Each soil sample was then designated by letter, number and depth, as one proceeds from surface to subsoil (table 1, col. 1). After the samples were taken at each natural soil horizon, a beaker of paraffin wax was melted and the sample containers emersed, thus sealing them from air and further contamination. The soils dilutions and plating out were executed approximately two hours after sampling. Although sealing the sample containers with wax does not completely prevent changes in numbers of microorganisms, the soils can be plated out at the same pH and moisture content as originally sampled. At the time of sampling, simultaneous measurements were taken on soil-surface temperature, soil-moisture content, soil evaporation, air temperature, soil organic matter, light intensity, and soil acidity (pH). The nature and extent of tree and herbaceous litter was also observed and recorded. The microclimatic installations (soil-moisture blocks, soil thermometer, and evaporation bulbs) were placed in approximately the same location as the microbial soil sampling stations. These installations provided additional data so as to correlate the fluctuation in population of soil organisms with the major microclimatic and edaphic factors in each experimental area.

Laboratory Procedure.—From the soil samples taken at two locations in Area G and Area P, respectively, composite samples were made to represent each horizon. Soil dilutions of each composite sample were prepared by the addition of 10 grams of soil to 1000 ml of sterile distilled water giving a dilution of 1:100. After the coarser particles had settled out after shaking,

successive transfers were made resulting in a series of dilutions of 1:1000, 1:10,000, and 1:1,000,000. All work was done aseptically. From these dilutions, 1 ml of each was dispensed by sterile pipettes into a selective medium and poured aseptically into sterile petri dishes. The cultures were incubated at 28°C. The bacteria and actinomycetes were permitted to grow one week or less before observations were made and the fungi were observed after four days. For bacteria and actinomycetes a Nutrose Agar was used as a medium;[2] for fungi, a Peptone Glucose Acid Agar was utilized.[3] Each dilution was run in duplicate both for bacteria and fungi, in addition to controls. The number of organisms computed from the plates represent the average values of three

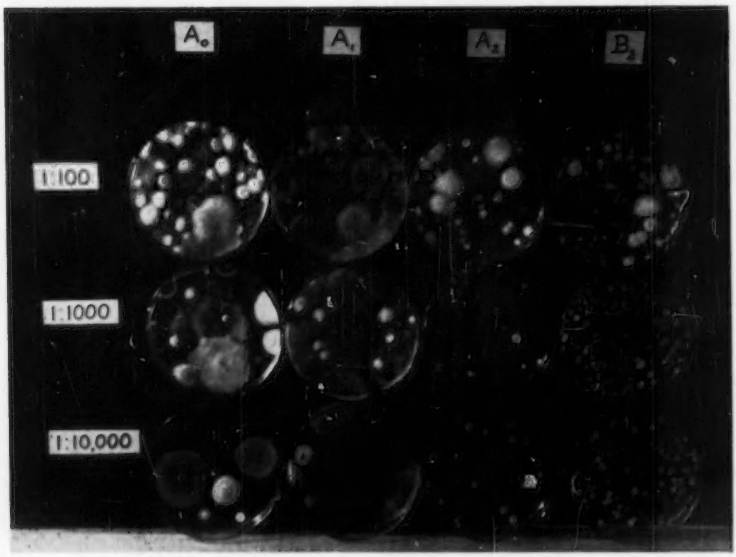

FIG. 1.—The relative numbers of fungal colonies by soil horizon and dilution in the area of good height growth of yellow poplar (Area G). Note the diminution in number of colonies with increased depth of the horizon until the B_2 horizon is reached. The larger number of colonies occurring in the latter horizon is significantly greater than in horizons A_1 and A_2.

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[2] Agar — $MgSO_4.7H_2O$
Nutrose — $FeSO_4.7H_2O$
Glucose — Tap water
K_2HPO_4 — Reaction pH 5.8

[3] Agar — Glucose
KH_2PO_4 — Distilled water
$MgSO_4.7H_2O$ — Reaction pH 5.0-5.4
Peptone

dilutions, or the average value of six individual plates for each soil horizon. Moisture contents were obtained for each horizon immediately before the isolations were made and the number of organisms present per gram dry weight of soil was computed, employing the plate count method. For each soil horizon, the acidity (pH) was obtained by the glass-electrode pH meter.

Several exemplary photographs of the plate-count were taken in order to illustrate the numerical distribution of microbes within each natural soil horizon (figs. 1-3). The number of organisms on each plate was counted by means of a microscope and counting plate. Only the 1:100, 1:1000, and 1:10,000 dilutions were used for statistical significance of numbers of organisms appearing on the plates. A determination of numbers of organisms was then made in order to compare quantitatively the difference in microbial counts between two portions of the same yellow poplar plantation. Results of these counts are here interpreted in terms of the principal factors which limit their distribution in the soil profile (table 1).

RESULTS

Total Abundance of Organisms.—The total relative numbers of all three classes of organisms investigated ranged from a minimum of 1000 fungi per gram to a maximum of 3,100,000 bacteria per gram of soil throughout the

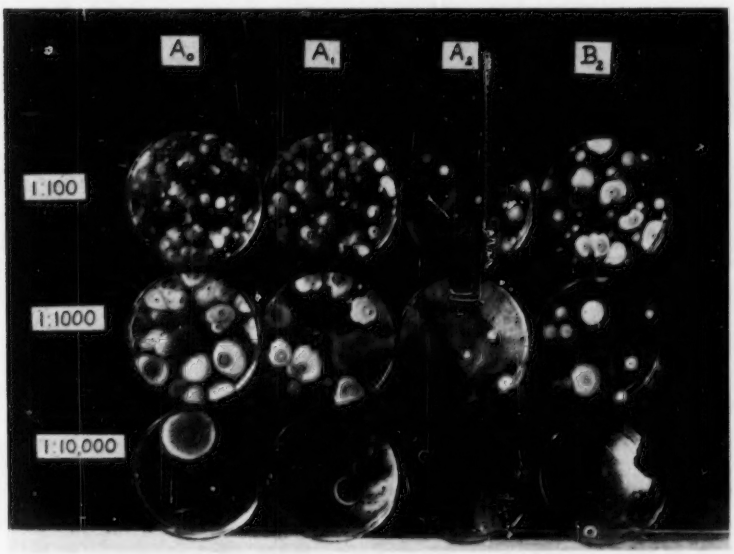

FIG. 2.—Relative number of fungal colonies by soil horizon and dilution in the area of poor height growth of yellow poplar. Area P, illustrated microbiologically above, has a slightly greater content of organic matter, greater porosity, higher water-holding capacity, greater acidity, and a narrower C/N ratio than Area G. Though this area supports a greater microbial population than the area of good height growth, the total profile differences are not significant.

course of the growing season. Of the three classes of organisms, the bacteria were found in greatest numbers, significantly greater than both the actinomycetes and fungi. Although the numbers of organisms fluctuated with the season, the greatest total number of bacteria and fungi occurred in Area P throughout the growing season. This numerical difference was not found to be statistically significant between the two height growth portions of the plantation. The markedly similar total profile quantities of fungi between areas is shown by comparisons of counts in figs. 1 and 2. Area G exhibited a 12 per cent greater total population of actinomycetes than Area P, but this also was not a significant difference. In general, the seasonal change in total numbers of organisms showed a maximum count in spring and early summer, a minimum during mid-summer, and a secondary maximum in early autumn (figs. 4-5). This cyclic fluctuation throughout the growing season occurred at varying intensities with all three classes of organisms studied. The total abundance of organisms was not high in relation to numbers of organisms found in similar soil types by various investigators. Although the total populations of fungi, bacteria, and actinomycetes were relatively similar for both experimental areas, there were certain significant and indicative intra-horizonal differences.

Intra-horizonal Abundance of Organisms.—The greatest number of fungi per gram of soil in each area occurred at the subsurface (B_2 horizon), where the number of colonies rises to a maximum of 16,710 per gram of soil. This

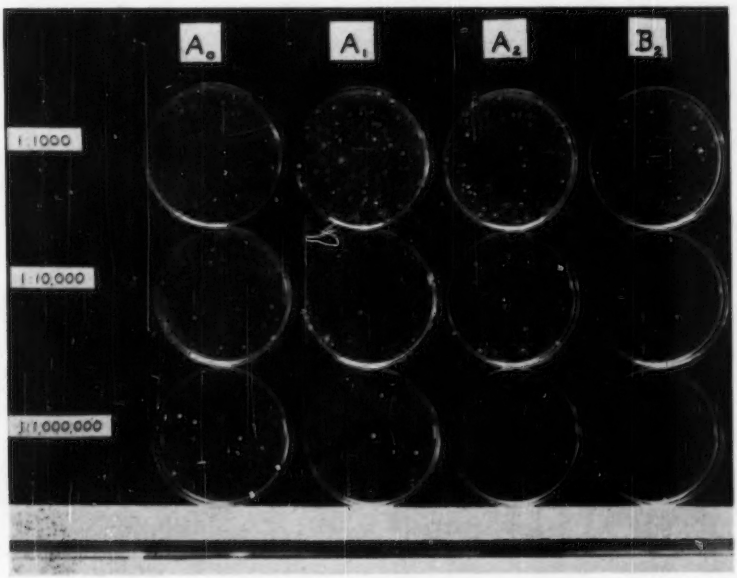

FIG. 3.—Bacteria and actinomycete colonies showing the relative density of organisms by soil horizon for the area of good height growth of yellow poplar (Area G). A nearly perfect correlation with increased depth of soil horizon is illustrated by this plate count. However, bacteria in the combined surface horizons (A_0 and A_1) were not significantly different than the numbers occurring in the subsurface horizons (A_2 and B_2).

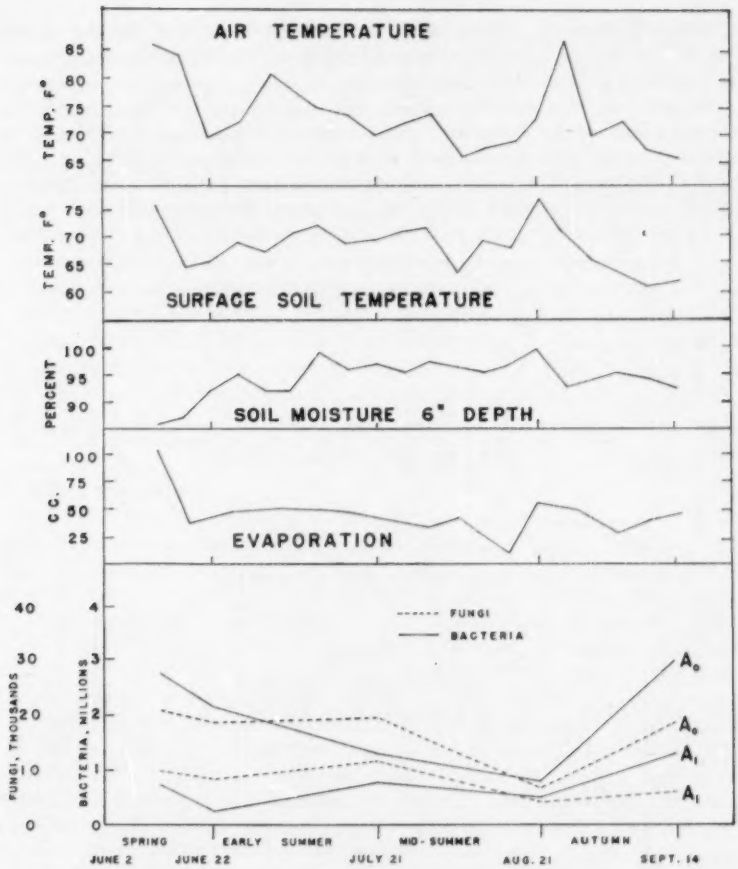

FIG. 4—The relation between numbers of organisms and microclimate in the area of good height growth of yellow poplar.

plate count was significantly[4] higher than in any other of the individual soil horizons in each experimental area (fig. 1). In both portions of the forest stand, the fungal population at the surface (A_0 and A_1 horizons) was highest in the spring and early summer, dropped to a minimum in mid-summer, and reached a secondary maximum in early autumn.

In contrast to the fungal population, the bacteria were found in greatest numbers in the combined surface soil horizons (A_0 and A_1). This numerical difference between surface and subsurface horizons was statistically significant in Area P.[4] In the area of good height growth the bacterial population in the surface horizons (A_0 and A_1) was not significantly different from the populations in the subsurface (fig. 3). The only seasonal fluctuation difference

[4] Statistically significant at 5 percent level of probability.

between height growth areas occurred at the beginning of the growing season. Bacteria reached their first maximum in spring in Area G, whereas in Area P the maximum was reached in mid-summer.

Influence of Microclimate.—Since the surface soil horizons reflect the external effects of the immediate environment, the quantitative correlation of organisms to soil and microclimate is particularly emphasized in the A_0 and A_1 soil horizons. The results indicate that the surface soil populations of bacteria were more sensitive to seasonal fluctuations than the fungi (figs. 4 and 5). In general, both bacteria and fungi in the surface horizons reached their

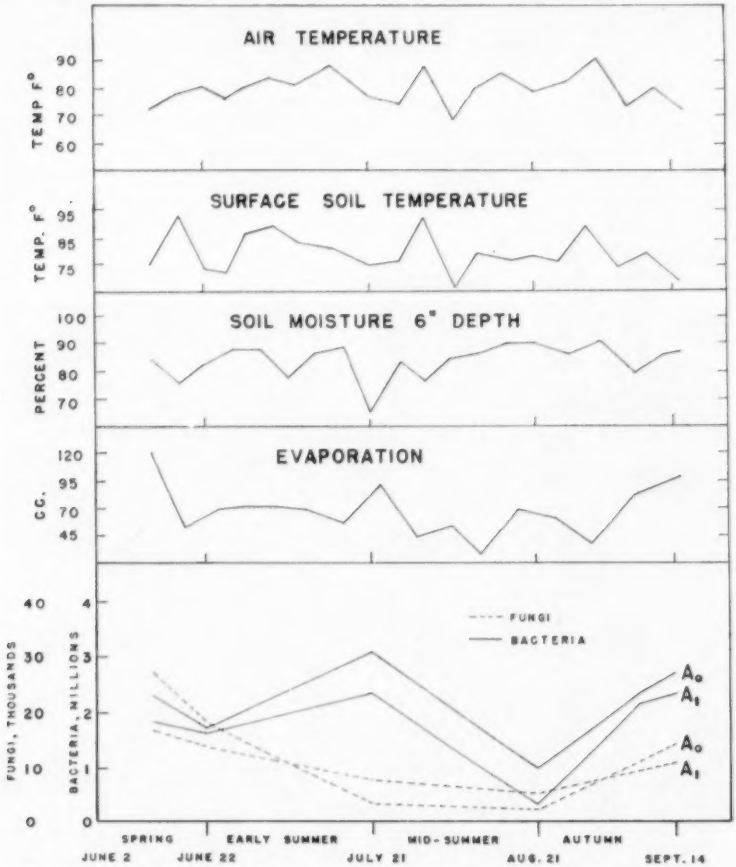

FIG. 5.—The relation between numbers of organisms and microclimate in the area of poor height growth of yellow poplar.

minimum numbers at a time when soil evaporation was least, when air and soil temperatures were lower, and when available soil moisture was highest. The more rapid cyclic bacterial fluctuation in Area P as compared to Area G

may be partially explained on the basis of the measured higher evaporation rate, higher air temperature, less available soil moisture, higher surface soil temperature, and greater light intensities of this site.

DISCUSSION

The number of organisms referred to in any specific soil horizon are only relative figures. They are constant only insofar as they represent the relative abundance of certain types of microbial cells at time of determination. It should be understood that there is no useful technique yet devised which accurately determines how much of the fungus material exists in the soil as mycelium or spores, by using the plate-count method (Waksman and Starkey, 1931).

With this limitation in mind, the fact remains that the greatest number of fungi (spores plus mycelia) were obtained at the B_2 subsurface horizon in both portions of the plantation. These figures represent not only a single instant of time, but are based upon many duplicate counts taken many times throughout the course of the growing season. It appears from this consistency that further study on the basis of horizon differentiation is not only justifiable but highly indicative.

It was not possible in this test to isolate all of the individual variables which might limit the number of organisms to a particular horizon. However, the combined factors of soil reaction, moisture, soil texture, organic content, porosity, and nitrogen content, were undoubtedly of primary importance in distinguishing the total fungi found in the B_2 from other horizons in the soil profile. Similarly, the bacterial counts in the surface horizons as distinguished from those in the subsurface, are principally a function of one or all of the same micro-environmental factors, but in differing magnitude. Since all soil horizons were very acid, and favorable to growth of fungi, it is unlikely that there was a sufficient range of acidities for this factor to be limiting the numbers of fungi by individual horizons. One of the principal variables, soil texture, appears to be closely associated with the marked difference in numbers of fungi between horizons. This likelihood is based upon the greater concentration of colloidal fine clay found in the subsurface B_2 horizons of both sites.

The combined edaphic factors reveal to a large extent the apparent *immaturity* of the forest insofar as organic decomposition of the surface horizons is concerned. This is further reflected by the relatively low total number of all organisms, and the very low percent of organic matter found.

Effects of years of injudicious cropping without proper fertilization of any kind is strikingly portrayed by the relatively low bacterial counts taken throughout the growing season. Similarity in total numbers of bacteria and actinomycetes for both Area G and Area P tends to point out (as with the fungal population) that these two portions of the same stand are essentially microbiologically similar, and that total organism equilibrium is being established at a low quantitative level in both sites.

The correlation between microclimatic factors and the surface soil horizons is markedly illustrated by bacterial counts taken in Area P. In this area of poor height growth, a significant difference between surface and subsurface horizons exists. Lacking the protective tree canopy and greater litter content as found in Area G, undoubtedly a more rapid organic decomposition is occurring in the surface horizons. This process is further aided by higher air and

soil temperatures, greater evaporation, lower humidities, and a set of climatic extremes which are conducive to surface decomposition.

CONCLUSIONS

This study was designed to estimate the total quantity and seasonal fluctuation of soil organisms, in soils supporting a 15-year-old yellow poplar plantation in southwestern Michigan.

Comparative estimates of total profile microbial numbers appears to be of limited value in the interpretation of forest site quality by direct means.

There are indications that numerical counts of soil organisms may have their greatest value as indices for interpreting the physical and chemical characteristics of individual soil horizons, and thereby indirectly influencing the growth of forest trees.

For valid interpretation on the quantitative counts of organisms, it is imperative that additional edaphic and micro-environmental data be obtained in support of the microbial estimates.

No direct relationship was found between numbers of bacteria, fungi, and actinomycetes, and the growth of immature stands of forest-grown yellow poplar.

Further research on the quantitative distribution of forest soil organisms may eventually lead to their practical application in instances where the populations can be controlled by cultural treatments. Under these conditions, numbers of organisms may well represent an index of fertility and plant growth.

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Pine Root Reaction in Sterile Culture to Mycorrhizal and Other Fungi[1]

K. D. Doak[2]

Crown Point, Indiana

Symptomatic details of fungus-root associations have been difficult to determine without growing the host plants in sterile culture with the suspected fungi. Due to difficulty in identification of fungi obtained in the mycelial stage by direct isolation from root tissues, most investigators have depended primarily on isolations made from internal tissues of young sporophores or the spores from mature sporophores. When sporophore formation did not occur, especially in connection with the endotrophic type of mycorrhiza development, direct isolations from the root tissues were the only resort. A sterile mycelium fungus, thus obtained from several species of *Vaccinium* and later grown seedlings in sterile culture (Doak, 1928) formed an endotrophic infection so closely resembling other forms of weak cortical parasitism that the association could not be considered proven. With an unmistakably characteristic sterile mycelium, however, Hatch (1934) demonstrated an interesting and unquestionable ectotrophic mycorrhizal relationship. Open culture inoculations as used by Stahl (1900) would be suggestive but otherwise unsafe. Circumstantial evidence based on visual association or connection of sporophores with a mycorrhizal system by Masui (1926) was likewise suggestive, but Melin's (1925) use of both sporophore isolates and sterile culture methods must be considered the most conclusive procedure.

The present study involves refinements and simplification of sterile culture procedures for growing plants and a comparative evaluation by examining the reaction of pine roots to several fungi.

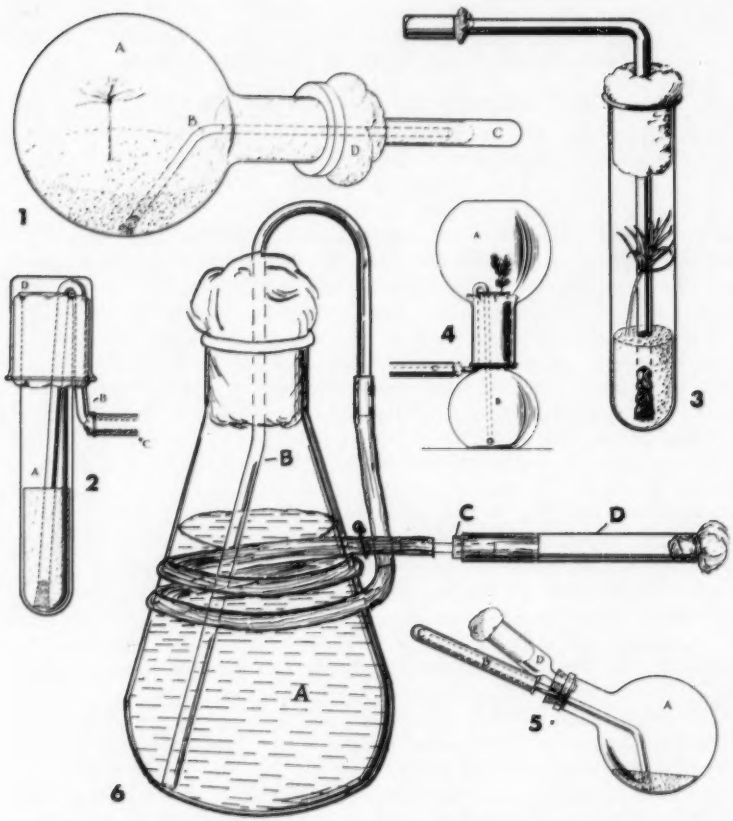
Acknowledgments.—The writer is indebted to Dr. Carl Hartley for many helpful suggestions and to Dr. N. A. Norton and Dr. P. L. Fisher for invaluable technical assistance.

Materials and Methods

Five styles of plant culture chambers comprising various modifications in construction embodied a common type of nutrient exchange tube and permitted the same operations with the same degree of safety as ordinary test tubes (figs. 1-5). These chambers and all accessory glass parts were of pyrex. Cotton plugs were rolled around the nutrient exchange tube for either an off-set or a central position in the mouth of the culture chambers (figs. 1-4), but in one type the large opening was closed by a rubber stopper and the nutrient additions made through one opening (fig. 5D) while suction operated through another (fig. 5B). In one type using two distillation flasks, the lower or small mouthed flask was completely filled with crystal grade silica quartz sand, but in all others the sand mass was one and one-half inches deep at center. Round cham-

[1] Investigation conducted at University of Pennsylvania, Department of Botany in cooperation with Allegheny Forest Experiment Station, Philadelphia, Pennsylvania.

[2] Formerly USDA, Bureau of Plant Industry, Division of Forest Pathology.



Figs. 1-6.—Sterile culture chambers for individual plants. 1. Two-liter round bottom with reinforced lip; 2. Two hundred fifty ml tube with lowered nutrient exchange tube; 3. Two hundred fifty ml tube with 90 degree nutrient exchange tube and vial as seal; 4. Combination 1½ and 2-liter flat bottom with lowered nutrient exchange tube; 5. Two-liter with nutrient addition funnel and suction tube through rubber stopper; 6. Three-liter Erlenmeyer for nutrient sterilization with rubber siphon tube and connections.

bers (figs. 1, 4, 5) were variously set up with two to five liter distillation flasks with reinforced lips while the rectangular chambers (figs. 2, 3) were 250 ml round bottom tubes. All nutrient tubes were covered by either vials or ordinary test tubes in which the plugging consisted of a single folded cut strip which permitted repeated removal and replacement during the nutrient addition, suction and flaming without danger of wadding. Ends of the nutrient exchange tubes at the bottom of the sand mass were plugged with glass wool to prevent drawing out the sand during suction after flooding with the nutrient solution.

A complete basic mineral nutrient solution (Hartwell and Pember, 1924) supplemented with 0.5 percent Trommer's malt for growth of the fungi was sterilized by autoclaving in three-liter Erlenmeyer flasks set up with a two and

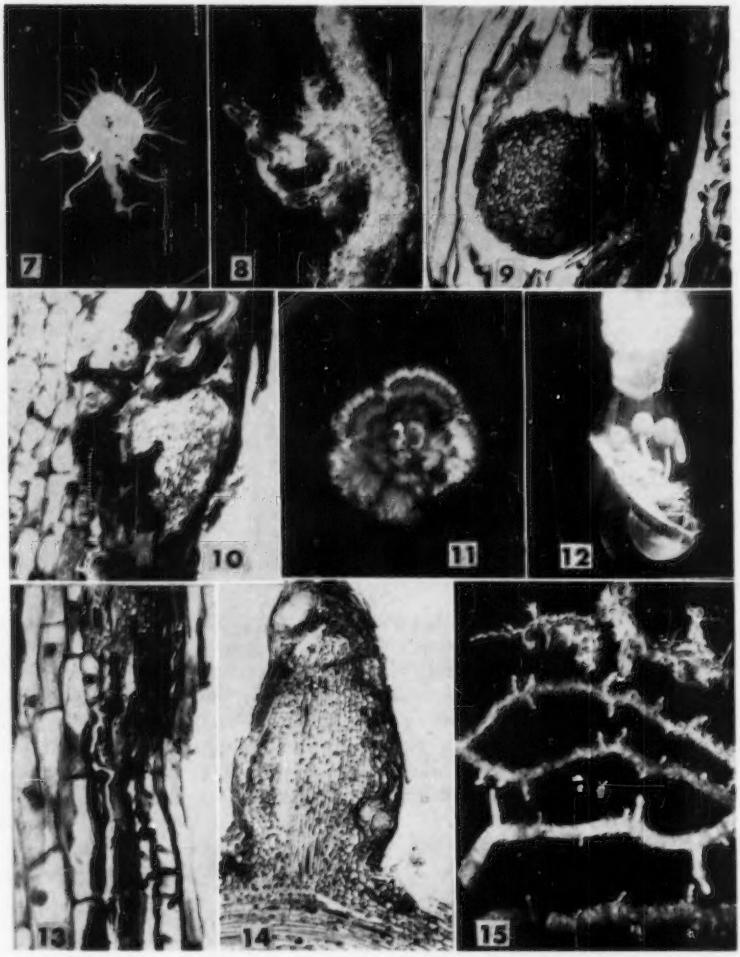
one-half foot rubber siphon tube (fig. 6B). The connection for attaching to the nutrient exchange tube of the plant culture chambers consisted of test tubes from which the ends were cut and fitted to the siphon tubes with rubber plugs (fig. 6C, D). All operations were conducted in a transfer chamber, the nutrient flask placed above the chamber and the siphon tube passed through a cotton plugged opening at one end. After removing plugs from the nutrient siphon tube connection and the nutrient exchange tube of the plant culture chamber, both were flamed and joined. Siphons were started by pumping with both hands. After flooding the sand mass, a suction pump was attached and operated until only the liquid held by capillarity remained. Both tubes were flamed and restoppered.

Seeds of *Pinus taeda* L. and *Pinus rigida* Mill. were surface sterilized by immersing in full strength superoxol for 30 seconds, then placed on 2.5 percent malt agar petri dishes at the rate of about 15 seeds per dish so that the seeds were separated. Washing was unnecessary since the surplus, active superoxol volatilized and left no toxic residues. Sterility of seed could thus be confirmed until germination after which single seedlings with three-eighths inch radicles were transferred to each plant culture chamber by removing the large plug supporting the nutrient exchange tube. A 14-inch glass rod with flattened end was used for this transfer and the fungus inoculum also transferred before flaming and replacing the plug. For the following three months, this plug was not removed. Transfer chambers with continuously operating steam jets were most dependable in all preceding operations.

Coprinus micaceus Fries was cultured from the internal tissues of young sporophores collected under a mixed oak stand near Huntingdon, Pennsylvania, *Armillaria mellea* (Vahl) Quel. from sporophores on a stump of *Quercus montana* Willd. near Mont Alto, Pennsylvania, AS 34-3 (sterile mycelium) from roots of *Pinus taeda* L. near Vineland, New Jersey, *Boletus miniato-olivaceus* Frost from sporophores under *Pinus taeda* L. near Smithfield, Virginia and *Boletinus pictus* Peck from sporophores under *Pinus rigida* Mill. near Greenbank, New Jersey. *Boletus miniato-olivaceus* Frost was here considered according to Peck (1889) although the color change and stem characters more closely approached *Boletus sensibilis* Peck. Many subsequent collections indicated that the species was extremely variable and that the variety *sensibilis* suggested in Peck's later report would best characterize the southern form. Young, vigorous subcultures were used as the source of inoculum for transfer to the plant culture chambers.

RESULTS

Armillaria mellea (Vahl) Quel. with *Pinus rigida* Mill. resulted in a combination of symptoms resembling the action of this fungus on other hosts in most respects. Although rhizomorphs penetrated the cortex of extending roots and caused some mechanical breaking of tissues (figs. 8, 9, 10, 14), there was considerable cortical infection by intracellular advance of scattered hyphae (fig. 13). Both kinds of infection induced extensive localization of tannin deposits and some evidence of tissue breakdown appeared in areas adjacent to infection. Sparse rhizomorph development occurred throughout the sand but there was a tendency for heavier and often intertwined masses



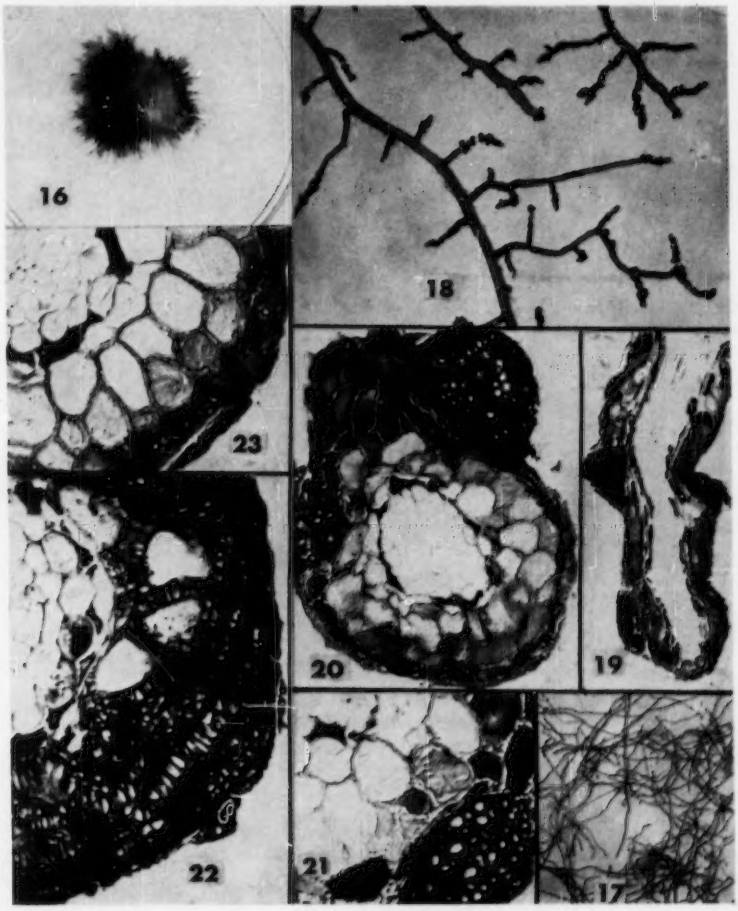
Figs. 7-15.—7. Culture of *Armillaria mellea* (Vahl) Quel. on malt agar; 8. Rhizomorphs attached to root of *Pinus rigida* Mill.; 9. Rhizomorph penetrating cortex; 10. Rhizomorph loop in cortex with heavy adjacent tannin deposits in cortical cells; 11. *Coprinus micaceus* Fries culture on malt agar; 12. Normal sporophore production on malt agar; 13. Scattered intracellular hyphae in cortex; 14. Rhizomorphs entering cortex at several points in root branch; 15. Roots of *Pinus taeda* L., from culture, showing scant mycelial growth along surface, unbranched absorbing roots with scattered root hairs, mycorrhizae absent.

along the root surface. All roots continued growth through the three months period of the experiment.

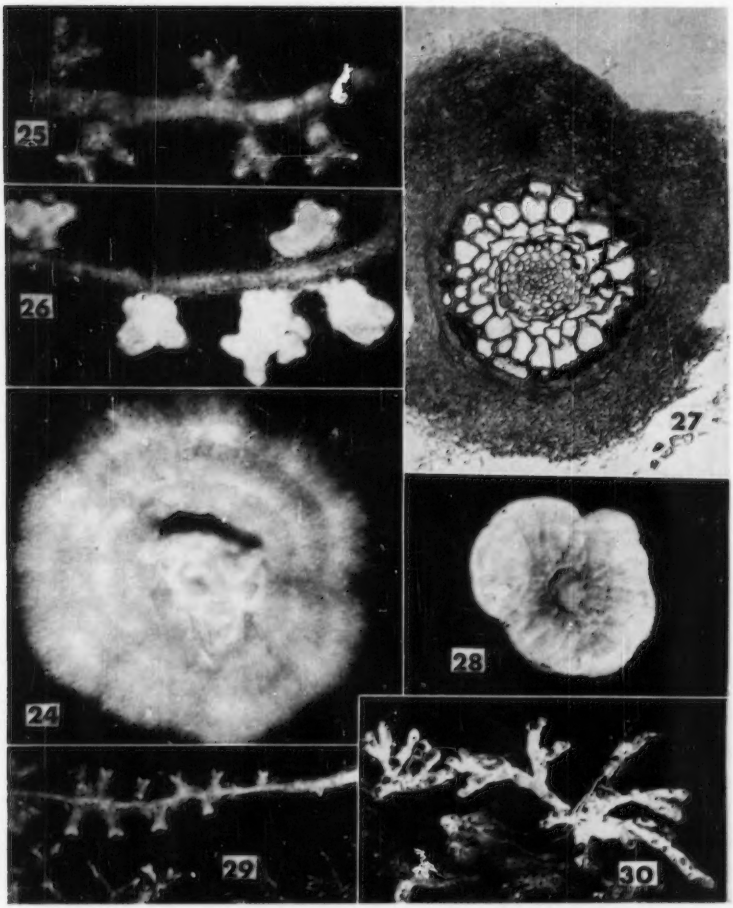
Coprinus micaceus Fries with *Pinus taeda* L. showed a uniform mycelial development throughout the sand and along the root surfaces (fig. 15). Evidence of root parasitism or mycorrhiza development was lacking. Absorbing

roots remained mostly unbranched with generally well distributed but sparse root hair development.

AS 34-3 (sterile mycelium) with *Pinus taeda* L. developed a thin mantle-like root sheath on all absorbing roots which had the general characters of a dark mycorrhizal mantle. There were prominent Hartig networks or intercellular, tightly compacted hyphae between the cortical cells (figs. 20, 23). Well-developed sclerotia-like bodies composed of thick-walled darkly staining hyphae were uniformly distributed over the surface of the absorbing roots



Figs. 16-23.—16. AS 34-3 (sterile mycelium) culture on malt agar; 17. Detail of hyphae from culture; 18. Root of *Pinus taeda* L., showing distribution of sclerotia; 19. Longitudinal section of mycorrhiza, showing thin mantle and sclerotia; 20. Transverse section with sclerotium and thin mantle; 21. Hyphae connecting sclerotium with Hartig network; 22. Converging sclerotia; 23. Mantle and intercellular Hartig network reaching third cortical layer.



Figs. 24-30.—24. Culture of *Boletinus pictus* Peck on malt agar; 25. Young dichotomous mycorrhizae on *Pinus rigida* Mill.; 26. Fully developed mycorrhizae; 27. Transverse section showing thick mantle and intercellular Hartig network; 28. Culture of *Boletus miniato-olivaceus* Frost on malt agar; 29. Young dichotomous mycorrhizae on *Pinus taeda* L.; 30. Fully developed mycorrhizae.

(figs. 18-21) but sometimes converged or overlapped to form a solid sheath of the same consistency (fig. 22). Hyphae of this fungus in culture showed dark, heavy walls (fig. 17) but sclerotia-like bodies were not formed.

Boletinus pictus Peck with *Pinus rigida* Mill. formed ectotrophic mycorrhizal mantles which developed as the absorbing roots dichotomized (fig. 25) and finally appeared as white masses with loose hyphal surface growth. In transverse section the Hartig network showed penetration to the endodermis (fig. 27). Growth of this fungus in the sand was sparse and lacked rhizomorph development.

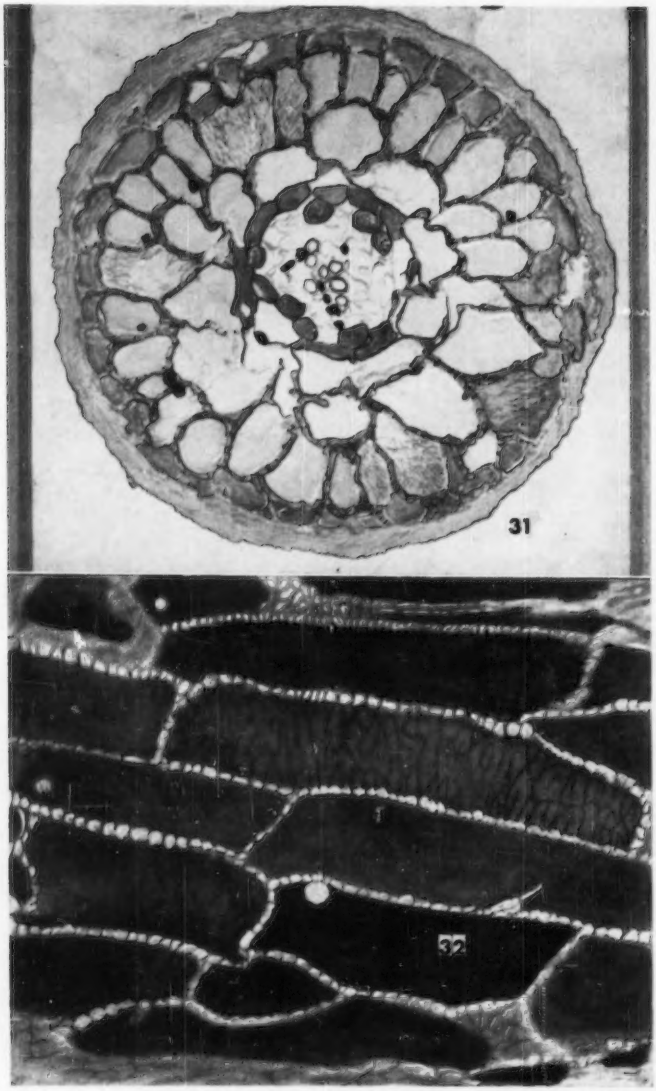
Boletus miniato-olivaceus Frost with *Pinus taeda* L. showed ectotrophic mycorrhizae with relatively thin mantles. Dichotomy of the absorbing roots followed closely their emergence, as the mother roots advanced, and became multiple before the mycorrhizal system was completed (figs. 29, 30). When fixed in 5 percent chromic sulphate in 4 percent formaldehyde saturated with salacylic acid then stained with a saturated solution of Orseillin BB in 1 percent acetic acid followed by 1 percent crystal violet in clove oil, the Hartig network showed variation in the extent of penetration but occupied most of the cortex (fig. 31). Mantles were compact and showed many loose white rhizomorph-like strands connecting with the mass of mycelium in the sand. When the Orseillin BB was used in a solution of 2 percent ferric citrate ($Fe_2(C_6H_5O_7)_2.6H_2O$) aqueous solution in the foregoing procedure, the Hartig network was more clearly demonstrated in both sectional and face view in the radial-longitudinal sections (fig. 32).

Reisolations after 3 months from 120 culture chambers showed 30 percent contamination which was not notably confined to any particular type of chamber. Since many operations by several individual operators were involved, especially in making nutrient changes, this was not considered excessive in comparison with less complex culture procedures. One type of chamber was found best adapted for handling in large numbers (fig. 1) due to ease of manipulation and the fact that it would stand balanced by the sand mass with the opening in a horizontal position while carrying out the various operations. This type could also be placed in rows on greenhouse benches whereas the other types required specially designed supporting racks.

DISCUSSION

Development of several types of infection under the conditions of this study indicated that pine roots react in markedly different ways to specific fungi. For pines in general, mycorrhizal reactions were found associated closely with certain characteristic morphological features of the root systems by Hatch and Doak (1933). The absorbing or short roots only become involved in the formation of typical ectotrophic mycorrhizal structures whereas the extending or mother roots remained free from infection. One exception has appeared, however, in the intricate proliferation at the ends of mother roots in certain localities noted by Doak and Fisher (1935). Such structures have been called compound mycorrhizae and externally have a nodule-like appearance although always produced by fungi. Mantle structure and development of the intercellular Hartig network was similar to the simple or dichotomously branched mycorrhizae of pines. It is uncommon for the mother or extending root to cease elongation and become a part of the mycorrhizal system.

Although *Armillaria mellea* (Vahl) Quel. infected only the extending or mother roots of *Pinus rigida* Mill. in this study, it attacks a wide variety of tissues in nature. Its activity under these cultural conditions was likely inhibited by temperatures much above optimum for strong mycellial and rhizomorph development as determined by Bliss (1946). The difficulty in classifying intermediate types of root infection was pointed out by Doak (1934) and has been further illustrated in the present study by the action of the sterile mycelium AS 34-3 on *Pinus taeda* L.



Figs. 31, 32.—31. Transverse section of *Boletus miniato-olivaceus* Frost mycorrhiza on *Pinus taeda* L. stained with Orseillin BB in acetic acid and crystal violet in clove oil, showing thin mantle and Hartig network; 32. Radial longitudinal section stained with Orseillin BB in 2 percent ferric citrate and crystal violet in clove oil, showing sectional and face views of Hartig network.

Design and adaptation of a nutrient exchange tube to procedures for individual plant sterile culture chambers tested in the present study was the prin-

cipal improvement over methods used heretofore by Melin (1925) and Klein and Kisser (1924). This made possible the removal of metabolic waste products of both fungus and root growth as well as chemical accumulations resulting from breakdown of the nutrient solution which have been heretofore suspected of toxic influence in confined artificial nutrient cultures.

SUMMARY

Several modifications in design and assembly of simplified sterile culture chambers for growing individual plants were tested with five suspected root fungi on two species of pine. Root reactions in the development of mycorrhizal and parasitic infections were compared. *Boletinus pictus* Peck and *Boletus miniato-olivaceus* Frost formed a type of Hartig network and mantle characteristic of certain pine mycorrhizae in nature. *Armillaria mellea* (Vahl.) Quel. produced rhizomorphs and an intracellular penetration resembling its previously reported parasitic behavior under natural conditions. A new combination of mycorrhizal and associated structures produced by AS 34-3 (sterile mycelium) on *Pinus taeda* L. was described.

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The Fossil Mosses of the Two Creeks Forest Bed of Wisconsin[1]

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During the spring of 1953 the exceptionally violent wave action of Lake Michigan along the Wisconsin shore, immediately south of the Door Peninsula, effected extensive erosion of the cliffs of glacial drift bordering the beach. Locally along these cliffs, the Two Creeks forest bed, with its abundance of subfossil coniferous and bryophytic materials, has long been known. With the large-scale erosion of the cliffs, an excellent new exposure of the forest bed resulted. In one place a particularly anomalous variation in the bed was found —where two distinct, seemingly identical organic layers exist instead of only one. The present report gives the result of a study designed to collect quantitative data on the frequency of the species of mosses in the forest bed both where this horizon exists as a single stratum and where the two organic layers are found. It was thought that in this way not only could information relative to the specific composition of the bryovegetation be established, but that perhaps botanical evidence to aid in an interpretation of the origin of the twin strata might be found.

Description of the Forest Bed

The Two Creeks forest bed, late Pleistocene in age, is a layer of macroscopic plant remains, among organic debris, 0.5-5.0 cm thick. In at least one place it appears to be double and consists of an upper and a lower stratum separated by a filling of silt (fig. 1). The lower stratum here is continuous with the bed where the latter is undivided. A thin layer of sand locally underlies the lower organic bed. Below this layer of sand, and directly below the stratum itself in those places where the sandy layer lacks, there are imperfectly varved red and gray glacial lake clays. A gray till (not visible in fig. 1), provisionally interpreted as Cary (Thwaites, 1953b), lies below the varved clays. Immediately above the upper bed, but again only locally, there is a layer, up to several feet in thickness, of sand and silt. This sandy deposit is overlain by the red Valders till.

The portion of the forest bed studied is situated in Manitowoc County,

[1] This work was in part supported by a grant from the Wisconsin Alumni Research Foundation. Sincerest thanks are expressed to Professor F. T. Thwaites who accompanied the author to the exposure, provided unpublished manuscripts on its geology and history, and gave many helpful suggestions. Professor W. C. Steere, the American authority on Pleistocene bryology, generously determined or verified some of the specimens. However, because Dr. Steere saw only a few samples and because the data in the present study are the result of numerous determinations, the author alone is to be held responsible for the statements made. The nomenclature of the fossil mosses follows that of Steere (1947).

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Fig. 1.—The Two Creeks forest bed at the locality where two organic strata are found. Above the upper organic bed (A) there is a layer of sand (B) which is covered by the red (Valders) clay (C). A layer of silt (D) separates the upper (A) and the lower (E) strata. Varved clays (F) are found immediately below the lower organic stratum. The recent slump (G) rests on the present beach (H) of Lake Michigan. Photograph by F. T. Thwaites, July, 1953.

Wisconsin (T 21 N; R 24 E; Sect. 2, N E 1/4). The organic stratum at this locality has already been the subject of one botanical report (Wilson, 1936). The areal extent of the bed is unknown, but organic debris has been encountered in well drillings throughout Manitowoc County and in all of the surrounding counties as well. Driftwood, however, is common in the overlying Valders till and a positive correlation of organic material recovered from wells to the Two Creeks bed is impossible.

HISTORY

The series of events surrounding the formation of the forest bed may be summarized as follows (after Thwaites, 1953a, b):

> During the retreat of the ice of the Cary or the third substage of the Wisconsin glaciation, the imperfectly varved clays below the bed were laid down. The level of Lake Michigan was then very high, in fact about 60 feet higher than its present level to judge from the deltas and the varved clays at Manitowoc. When the ice had finally retreated far enough to free not only the Straits of Mackinaw, but indeed the entire St. Lawrence valley, the lake fell to at least its present level. Previously inundated land was exposed and a spruce forest grew at an elevation only slightly above the present level of the lake —an indisputable testimony to the low level of the lake at that time. The development of the forest marks the Two Creeks Interstadial.

With the advance of the Valders ice, the fourth Wisconsin substage, drainage to the northeast was blocked and the lake level again rose. The forest was progressively inundated, and silt and sand were deposited in it. Under such unfavorable circumstances the trees could not long survive and the death of the forest must certainly have preceded its being overridden by the advancing ice. Just how long the forest existed is not known, but Wilson (1936) has found no logs *in situ* with more than 80-120 growth rings. An average age of the organic debris from the bed has been estimated by the carbon$_{14}$ method to be about 11,000 years (Arnold & Libby, 1950).

PREVIOUS STUDIES

Cheney, who determined the mosses in Wilson's collections from Two Creeks, recorded 19 species (Cheney, 1930, 1931). The only other cryptogamic plant found, a bracket fungus, has been assigned to the genus *Polyporus* (Wilson, 1932). The remains of higher plants include an abundance of woods, twigs, and some cones of *Picea mariana* (Mill.) B.S.P. and perhaps of *P. glauca* (Moench.) Voss (Wilson, 1936). Although pollen grains of grasses, heaths, birch, and jack pines and spores of an *Asplenium* have been reported (Wilson, 1932), no vegetative parts of these plants have been discovered *in situ*.

METHODS

A fresh exposure was made with a shovel along the bed where only a single layer exists, and 30 samples of the organic debris were taken, the interval between the sampling points being about 12 inches. Fifteen samples were collected in a like manner from the upper layer of the apparently double bed, and 15 were taken from the lower. Although an attempt was made to collect the same amount of material in each sample, the samples were later found to range in weight from 236 to 265 grams. At the time of collection the organic material was not examined for fossil mosses and no samples were rejected in the field or in the laboratory because of the lack of such fossils.

In the laboratory each sample was inspected and any mosses removed. The specimens were placed in a dish of water and gently agitated to remove adhering materials. No unusual chemical or physical methods were employed to extract the fossils. For each sample the species of mosses present were recorded, but no attempt was made to estimate abundance. The presence of spruce needles was also recorded. Permanent slides of each moss species in a given sample, save the easily recognizable *Ditrichum*, were prepared by mounting

specimens in "Viscol" (Dahl, 1951). All of the slides thus made to substantiate the determinations upon which the data are based are in the author's herbarium. In addition, a complete set of specimens of the eight mosses recognized are on deposit in the herbarium of the University of Wisconsin. Other sets, lacking only the rare *Calliergon turgescens*, have been placed in the herbaria of Dr. W. C. Steere, The University of Cincinnati, The Chicago Museum of Natural History, The Farlow Herbarium of Harvard University, and Le Laboratoire de Cryptogamie du Muséum d'Histoire Naturelle (Paris).

Because much of the material is fragmentary or poorly preserved and because all of it is sterile, there has been no attempt to make fine taxonomic distinctions. Specimens of the polymorphic genus *Bryum* are not segregated to species, but forms diverse enough to include *B. bimum* (Brid.) Turn., *B. cyclophyllum* (Schwaegr.) B. & S., and *B. pseudotriquetrum* (Hedw.) Schwaegr., all reported by Cheney, are present. Hypnaceous mosses with broadly lanceolate, non-squarrose leaves have been assigned to *Brachythecium salebrosum* (Hoffm.) B.S.G. on the basis that most of the specimens thus delimited actually belong to this species. It is not impossible, however, that some poorly developed or badly preserved material of *Camptothecium nitens* (Schreb.) Schimp. has also been included in this definition. Hypnaceous mosses with falcate-secund leaves have been called *Drepanocladus uncinatus* (Hedw.) Warnst. again because most of the specimens fitting this description appear to belong to this species. Several other species of *Drepanocladus* have been reported by Cheney.

RESULTS AND DISCUSSION

The fossil mosses and the spruce needles occur in the three sampled portions of the organic layers with the frequency distribution recorded in table 1. From this table it can be seen that the mosses are restricted to the simple bed and to its continuation as the lower layer of the double bed. No fossil mosses exist in the upper stratum. The only fossils common to all three of the portions sampled are spruce needles and coniferous wood although the presence of the latter was not recorded.

TABLE 1.—The percent frequency of the species encountered in each of the three sampled portions of the organic strata (percent frequency = the number of samples in which a species is found/total number of samples × 100). The simple bed is represented by 30 samples, the lower and the upper strata of the "double" bed by 15 samples each.

	Percent Frequency		
	Simple Bed	Double Bed	
		Lower	Upper
Abietinella abietina (Brid.) C. Müll.	3	27	....
Brachythecium salebrosum (Hoffm.) B. S. G.	70	53	....
Byrum sp.	43	60	....
Calliergon turgescens (Th. Jens) Kindb.	3	....	....
Campylium stellatum (Hedw.) Lange & C. Jens	73	20	....
Ditrichum flexicaule (Hoffm.) B. S. G.	83	73	....
Drepanocaldus uncinatus (Hedw.) Warnst.	50	80	....
Tortella tortuosa (Hedw.) Limpr.	63	20	....
Spruce needles	100	100	100

Now from fig. 1 it might be assumed that there are actually two separate forest beds at the locality photographed. The distribution of the fossil mosses leads to a better explanation: The upper organic layer is not a forest bed *in situ* and only the lower stratum represents the true forest bed. The materials of the upper stratum are transported or at least reworked. At the time of the progressive inundation of the forest, during the Valders advance, silts were deposited on the forest floor. The mosses anchored there and some of the coniferous materials were covered and imbedded. Some needles, twigs, and branches from the spruce trees, however, could float about freely. An accumulation of this free-floating but probably ponded debris was subsequently covered with a heavy layer of sand to form what now only appears to be a double forest bed.

Of the eight taxonomic entities recognized, *Abietinella abietina, Brachythecium salebrosum, Tortella tortuosa,* and *Drepanocladus uncinatus* are not to be found in Cheney's lists. Of these species, however, the *Abietinella,* relatively infrequent in the stratum yet a species not easily confused with others, appears to be the only one unquestionably new to the flora. The more common *Brachythecium salebrosum* and *Tortella tortuosa* may have been encountered by Cheney and reported under different names. Certainly our broad definition of *Drepanocladus uncinatus* includes at least some of the members of this genus listed by Cheney, but specific determinations in the highly variable *Drepanocladus,* and particularly in Pleistocene materials, are, by the very nature of the taxonomy here, inevitably ambiguous.

Although only two of the fossil mosses, *Ditrichum flexicaule* and *Calliergon turgescens,* have not been reported in the modern bryoflora of Wisconsin (Cheney & Evans, 1946), none of the other six species find optimum development in the state today. Instead, all are to be associated with floras of more northern affinities and are common in a vegetation that is ". . . one of neutral to calcareous meadows or lake shores, and is still found from northern United States to Alaska" (Steere, 1954). For example, some of the present-day plant communities of the northern Mackenzie Basin of Canada described by Lindsey (1953) include mosses found as fossils at Two Creeks.

FOSSILIZATION OF CRYPTOGAMS

Steere (1942) has developed an argument to explain the primary requisites for the fossilization of bryophytes. His hypothesis may be summarized as follows:

> The consistent paucity or entire lack in the fossil record of certain species, genera or even whole groups of bryophytes cannot be explained by chance alone. The rarity of fossil bryophytes in general and the absence of certain ones in particular can be related to the chemical nature of the cell walls of these plants. Unlike the cellulose-rich cell walls of the higher plants, those of the bryophytes are made up largely of the relatively readily hydrolyzed hemicelluloses; the lignins, compounds with an abundance of aromatic rings, plentiful in the cell walls of most higher plants, are known in the bryophytes, but they are generally less abundant here than in the phanerogams. Aromatic constituents, considered to be lignin derivatives, have been shown to be more plentiful in species of moist habitats than in those of drier places. It is known that certain of these aromatic compounds are toxic to some microörganisms. Much contemporary opinion favors the notion that lignin and lignin derivatives, rather than cellulose, are the materials which accumulate under anaerobic conditions in the formation of peat. It would be essential then, for the preservation of mosses, that the plants be deposited in water and that their cell walls contain lignin or aromatic constituents. If the foregoing assumptions are correct, the

hydrophilic mosses will be the most frequently preserved both because they contain more lignin than mesic species and because the opportunity of their being deposited in water is greater. That hydrophilic mosses are more common in the fossil record than are species of more mesic habitats is actually true.

Just as it would be fallacious to assume that the eight fossil mosses represent the only species of bryophytes in the original vegetation of Two Creeks, so would it be erroneous to assume that in that original vegetation the mosses were the only cryptogams present. In modern plant communities in which these mosses are members, lichens also abound. Lichens as well as bryophytes must indeed have existed in the Pleistocene vegetation of eastern Wisconsin.

As testimony to the rarity of fossil lichens, it appears that no fossils of this group have been recorded from Pleistocene strata in North America (although one or two reports of fossil lichens in earlier strata do exist). In northern Europe, however, at least one study of post-glacial deposits indisputably containing subfossil lichens has been made (Sernander, 1918).

Like those of the bryophytes, the cell walls of lichen hyphae contain little if any cellulose but instead are composed mostly of certain homopolysaccharides (e.g., chitin and lichenin) and hemicelluloses. The presence of lignin in some hyphal walls was early recorded by Schellenberg (1896) on the basis of a phlorglucinol-hydrochloric acid test. This report was subsequently challenged by Tobler (1925). As a supplement to an exploratory investigation of an indirect method for lignin determination involving calculations from iodine numbers (Kürschner & Wittenberger, 1939), a brief analysis of several mosses and lichens revealed that lignin is doubtless present in the former and possibly in the lichens as well. Even if the presence of lignin in hyphal walls were established beyond question, however, the occurrence of the substance in the lichens could never compare quantitatively with that in the phanerogams or probably even that in the mosses. Nevertheless, aromatic constituents—most of the lichen acids—are found in all but a few of the genera and some of these acids have been shown to be of antibiotic nature.

If it is true that the presence of lignin is the *sine qua non* for the preservation of plant parts under anaerobic conditions, then the rarity of lichens in fossil-bearing strata would be largely explained. Although qualitative analysis in lichen chemistry has been perfected to a relatively high level, little is known of the quantitative occurrence of aromatic compounds in individuals. It is obvious that a differential preservation unfavorable to the lichens has occurred, but more definitive explanations, necessarily at a physiological level, are as yet impossible.

Although some studies have been made on the rate of decomposition of the several parts of the cell wall in the higher plants (e.g., Barghoorn, 1949) and many have been made on the nature of the degradation of commercially important woods under anaerobic conditions, the question of the relative rate of decay of the thallus in different groups of the cryptogams is largely unexplored. The results of a few observations made by the author on the decomposition of some lichens and mosses seem of sufficient interest to warrant mention.

Ten samples each about 2 cm long of each of ten species of lichens and ten of mosses were collected from a variety of non-aquatic habitats in northern Wisconsin. To minimize genetic differences in the samples, the specimens of each species were taken from a single plant or a small colony. Each of the

200 samples, in the fresh condition, was attached with thread to tiers of wire mesh which were placed in an ordinary covered five-gallon aquarium filled with water from a local lake rich (?) in microörganisms. The water level was main-

TABLE 2.—The percentage of the samples of groups of lichens and mosses not decomposed after the indicated cumulative time lapse in days from the start of the observation.

Time lapse in days	88	105	120	134	154	168	245
A. 80 lichen samples, 8 species:*	95	55	38	19	5	0	0
B. 20 lichen samples, 2 species:*	100	100	100	100	100	100	100
C. 100 moss samples, 10 species:*	100	100	100	100	100	100	100

* The species are: (A) *Alectoria jubata* (L.) Ach., A. *nidulifera* Norrl.: *Cetraria atlantica* (Tuck.) DR., *C. ciliaris* Ach., *Evernia mesomorpha* Nyl., *Parmelia caperata* (L.) Ach., *P. physodes* (L.) Ach., *Usnea cavernosa* Tuck.; (B) *Cladonia sylvatica* (L.) Hoffm., *Peltigera canina* (L.) Willd.; (C) *Bartramia pomiformis* Hedw., *Calliergon cordifolium* (Hedw.) Kindb., *Climacium americanum* Brid., *Dicranum drummondii* C. Müll. det. Conard, *Hedwigia ciliata* (Ehrh.) Hedw., *Heterophyllium haldanianum* (Grev.) Kindb., *Leucobryum glaucum* (Hedw.) Schimp., *Neckera pennata* Hedw., *Polytrichum ohioense* Ren. & Card., *Sphagnum warnstorfii* Russow. det. Lawton comm. Conard.

tained constant by the addition of distilled water when necessitated by evaporation. The pH (Beckman meter) of the water remained 7.5-7.8 throughout the eight months of observation.

Observations were made periodically by removing the wire tiers and by counting the number of undecomposed individuals of each species. A plant was considered decomposed when its form was lost and only a pulpy globlet, or indeed nothing at all, remained. A minimum of subjective judgment was required for these determinations because the interval between counts was rather long.

The results are given in table 2. The first group of eight lichen species, habitually epiphytic in Wisconsin, all decomposed relatively rapidly. Of the second set, none of the individuals of the two primarily soil-inhabiting lichens decomposed during the period of observation. None of the 100 specimens of the 10 species of mosses, including both epiphytic and non-epiphytic species, decomposed during the period of observation. Moreover, at the end of the eight-month period, of these 100 specimens 42, distributed among six species, had produced weak but actively-growing shoots of which a few attained a length of 5 cm. Wilson (1932) has mentioned the "thin and scraggly" branches of some of the fossil mosses that he collected for Dr. Cheney, and similar shoots are to be found in the material of the present study. Concerning such shoots, Dr. Steere writes (1954): "The small branches that mosses send out when submerged are the bane of our lives now, since much of the fossilized material consists of such abnormal growth forms; there is no doubt that the preservation was done under water."

The author is fully aware of the short-comings of the procedure used to obtain the results reported above. The magnitude and the very nature of the difference in the behavior of the lichens and the bryophytes observed in an artificial, anaerobic environment, however, cannot fail to stimulate the imagination in evaluating the significance of the present assemblage of fossils.

ABSTRACT

The Two Creeks forest bed, an organic stratum of late Pleistocene origin in eastern Wisconsin, was sampled to obtain data on the frequency of the fossil mosses. The resultant information on the distribution of the eight entities recognized among the mosses suggests an explanation of the origin of an abnormality in the stratum where in one place two organic layers exist instead of only one. The lack of lichens in the fossil assemblage at Two Creeks and the extreme paucity of fossil lichens in general is noted and the lignified cell wall as a requisite for preservation is discussed. The results of a set of simple observations on mosses and lichens subjected to an artificial anaerobic environment indicate that whereas most of the lichens decompose relatively rapidly, the mosses not only resist decay but may actually continue growth.

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Observations on Open-Grown, Non-Native Conifers in Southern Illinois

Leon S. Minckler[1]

The original forest cover of southern Illinois was composed of hardwood species, chiefly oaks and hickories.[2] Farming over the past century has caused depletion and erosion on the steeper slopes and forced a large area to be withdrawn from cultivation. Perhaps ¾-million acres of this abandoned, now open land is best suited for forest crops. In their depleted condition, however, most of the soils will not support the best native hardwoods.

For reforestation purposes, foresters have used conifers, chiefly shortleaf pine (*Pinus echinata* Mill.) and loblolly pine (*Pinus Taeda* L.). Many thousands of acres in southern Illinois have been successfully planted to these species and good survival and high yields at early ages are common (Boggess, 1953; Minckler and Deitschman, 1953). Although early success is expected, the *ultimate* development of the trees is still unknown because there are no plantations more than about 20 years of age in this area.

The purpose of this paper is to summarize observations on many individual non-native conifer trees much older than the plantations established during the past 20 years. The development of these older trees may indicate the response of these species to climatic and edaphic factors. This information should be useful in predicting the future development of recently established plantations. It is well known that exotics or species far from their native range may develop abnormally. Often trees are unusually short (Lorenz and Spaeth, 1947) and may exhibit some unusual physiological reaction, such as susceptibility to freeze damage (Minckler, 1952).

Observations Made

Large conifers of advanced age, as well as younger trees, have been observed throughout southern Illinois growing in yards, cemeteries, and along roadsides. Usually they were planted on uneroded soils, better than the average abandoned old field. Measurements were made on 61 of these planted trees, including 9 different species. None of the species was native to the area where it was growing.

The following measurements and observations were made on each tree (Where groups of several trees occurred in the same place, only the tallest was measured.): (1) Trunk diameter in inches outside bark at 4.5 feet above ground; (2) Total height of tree in feet; (3) Annual ring count to determine age; (4) On some trees an analysis of annual rings to determine the past growth pattern of the tree; and (5) Current height growth (whether it has stopped or is continuing).

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[2] Shortleaf pine occurs naturally in Illinois only on the steep west-facing Mississippi River bluffs in the extreme southwestern portion of the State.

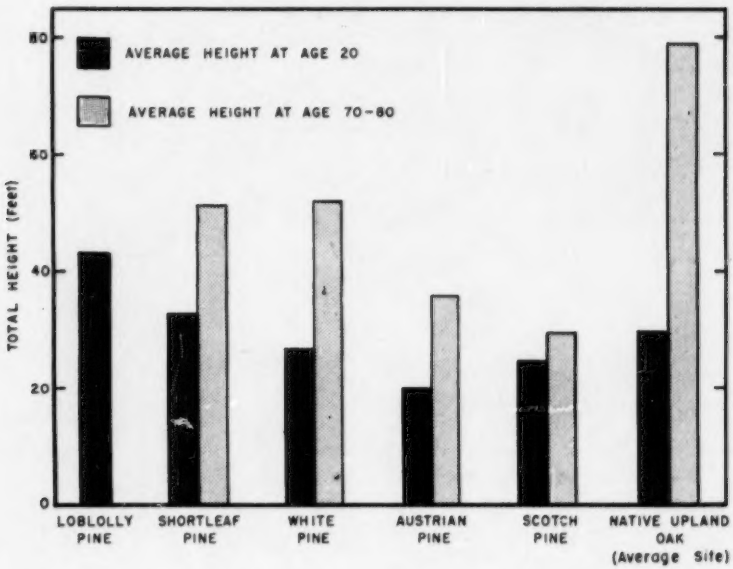

Fig. 1.—Heights of non-native conifers compared with height of native upland oak.

HEIGHT GROWTH

The early height growth of the open-grown conifers in southern Illinois was good (fig. 1). Except for the exotics — Austrian pine (*Pinus nigra* Arnold) and Scotch Pine (*Pinus sylvestris* L.) — height growth was comparable to that of native upland oak (Schnur, 1937). According to recently published data (Coile and Schumacher, 1953), the open-grown loblolly and shortleaf pine would be expected to grow to a height of 75 and 55 feet, respectively, in 50 years. White pine (*Pinus Strobus* L.) height at age 20 corresponds to a height of more than 90 feet at age 50 when based on curves for natural stands in the Lake States (Brown and Gevorkiantz, 1934).

These predicted future heights of the non-native conifers, based on early growth, suggest relatively tall trees at maturity. Actual measurements, however, show that later growth is sharply reduced. This agrees with the findings of Lorenz and Spaeth (1947) for plantations on prairie soils of central Illinois. They found that the total heights of dominant trees at age 68 in plantations on prairie soils were: white pine — 61 feet, Scotch pine — 43 feet, Norway spruce (*Picea abies* (L.) Karst.) — 61 feet, and European larch (*Larix decidua* Mill.) — 64 feet.

Judging by height curves for natural white pine stands in the Lake States, the planted white pine trees at age 15 appeared as if they would attain a height of 90 feet at 50 years. But actually those studied attained less than half that height in 50 years. The other species followed similar trends.

In the present study, the exotic species made from 55 to 80 percent of their total height growth during the first 20 years. Shortleaf pine attained 65 percent and white pine 52 percent of total height in the first 20 years. Native oak, on the other hand, grew only 38 percent of its total height during that period. Three red pine trees (*Pinus resinosa* Ait.), one pitch pine (*Pinus rigida* Mill.) and one white spruce (*Picea glauca* (Moench) Voss), and two American larch (*Larix laricina* (Du Roi) K. Koch) had final heights of 48 to 62 feet.

Fig. 2.—Characteristic bent main stem shown on dead top of Austrian pine. There was no relationship between direction of bending and direction of prevailing winds.

Height growth stoppage of the conifers examined generally came about in one of two ways: (1) The main stem lost its vertical position and grew horizontally or assumed a slightly hooked form (fig. 2). This was probably caused by the death of the terminal bud and the dominant growth of one lateral to form an apparent continuation of the main stem. (2) The terminal stem lost its dominance and several other shoots grew at a broad angle to the main, vertical stem (fig. 3) Such behavior suggests that the crowns of these species, when growing in southern Illinois, do not obtain enough water and nutrients to support height growth beyond that shown. This agrees with the explanation of height growth given by Busgen and Munch (1931).

There is, of course, the question of whether or not the maximum height of open-grown trees is a fair criterion for forest-grown trees. Although the *rate* of height growth may differ, it is assumed that *ultimate* height, unless strong, persistent winds are a factor, would be about the same whether trees grew in stands or singly. Observations over many years indicate that large, old, open-grown native trees are about as tall as nearby stands on similar soils. For example, open-grown oak and elm in southern Illinois have been observed to be 90 or more feet tall on sites where stands of those species do not exceed that height. Similar observations on native pine in the South have also been made. Another case in point was noted in a cemetery near Nashville, Illinois (fig. 4). An eastern redcedar (*Juniperus virginiana* L.) aged 55 was 47 feet tall. Next to it, an Austrian pine aged 73 was only 35 feet tall. An open-grown native hickory, about 20 feet away, was 80 feet in height. Both the hickory and cedar were still growing but the Austrian pine had virtually ceased height growth. So open-grown trees appear to give a fair indication of final heights to be expected for a given situation.

Fig. 3.—A group of white pine showing the typical loss of dominance of the central stem and the cessation of height growth. The largest tree to the left is 25 inches in diameter, 53 feet tall, and 70 years old.

Fig. 4.—From left to right: Native hickory, native eastern redcedar, and exotic Austrian pine. The Austrian pine is 35 feet tall and 73 years old; height growth has virtually ceased. The cedar is 47 feet tall and 55 years old, and the hickory is 80 feet tall. Growth is continuing on both the cedar and the hickory.

DIAMETER GROWTH

The rate of diameter growth for the open-grown trees exhibited the same sharp reductions as height growth. This is shown by comparing old and young

trees (table 1) and by counting growth rings on several old trees of four species. Shortleaf pine, for example, grew to 13.8 inches diameter in 25 years and then only 5.6 additional inches in the next 42 years. Thus, during early growth, there were 3.6 growth rings per inch of stem radius. In the later period, there were 15 rings per inch. This rather abrupt slowing of diameter growth held for all the species studied. Abrupt slowing of growth does not ordinarily occur in open-growth native hardwoods of the region. Its occurrence suggests the presence of climatic or edaphic factors that tend to limit the growth of these non-native and exotic conifers. Deitschman and Lane (1952) found similar abrupt slowing of diameter growth for several species of non-native conifers planted on coal-stripped lands in Indiana.

SIGNIFICANCE OF RESULTS

Previous experience and studies have shown that planted shortleaf and loblolly pine will survive well and make good early growth on old fields in southern Illinois. The present observations show that shortleaf pine and white pine, when planted on uneroded sites around houses or cemeteries, reached final heights of 50-60 feet and diameters of 18-25 inches in 70-80 years. The exotics, Scotch and Austrian pine, did much poorer. There are insufficient data

TABLE 1.—Diameter and diameter growth by species and tree ages

Species	Old trees (height growth stopped)				Young trees (height growth continuing)		
	Trees measured	Aver. d.b.h.	Aver. age	Aver. diam. growth per decade	Trees measured	Aver. age	Aver. diam. growth per decade
	No.	In.	Yrs.	In.	No.	Yrs.	In.
Loblolly pine	—	—	—	—	5	18	6.1
Shortleaf pine	7	18	72	2.5	6	19	4.2
White pine	14	21	69	3.0	3	27	4.7
Austrian pine	9	19	73	2.6	4	27	4.1
Scotch pine	5	16	47	3.4	1	17	3.7
Red pine	3	25	82	2.9	–	—	—
Pitch pine	1	22	78	2.8	–	—	—
Spruce	1	25	78	3.2	–	—	—
Larch	2	19	73	2.6	–	—	—

for larch, spruce, pitch pine, and red pine to draw any conclusions. It appears that shortleaf pine, white pine, and presumably loblolly (although no large loblolly trees were found) in this region will grow to 18-20 inches in diameter and have a usable trunk length of about 20-24 feet on average or better sites. However, they probably will not grow to the height attained in their native habitats; diameter growth may decrease rather abruptly at about 20-35 years of age; and the trees may be subject to abnormal damage from insects, disease, or weather. These species should be planted according to site requirements, and the source of seed should be as close as possible to the place of planting.

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Vegetation of the Huachuca Mountains, Arizona[1]

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During the course of two years (1949-51) of wildlife studies in the Huachuca Mountains of southeastern Arizona considerable attention was given to the distribution of plant communities as a background for faunal investigations. Intensive ecological studies of plants were not possible because of prior duties but a rather complete analysis was made of major vegetation units. Continuing biological studies in the Huachucas seem to justify making those observations available to other workers.

The Huachuca Mountains lie in southeastern Arizona approximately 25 miles east of the city of Bisbee, Cochise County. This area is in the Mexican Highland Section of the Basin and Range Physiographic Province. The southern extremity of the range is intersected by the International Boundary and from this point it extends northwesterly about 20 miles, having a southeast-northwest axis.

Acknowledgments.—The author is greatly indebted to Mr. L. N. Goodding for the opportunity to profit from his long years of experience with the flora of southeastern Arizona. His taxonomic and distributional studies of plants of the Huachuca Mountains, while he and the author were employed on the Huachuca Wildlife Area by the Arizona Game and Fish Commission, provided a background for the present paper.

Mr. Goodding's collections during that period, including approximately 500 species of plants, were deposited in the herbarium of the University of Arizona, Department of Botany and Range Ecology.

In addition to the basic field studies, Mr. Goodding lent invaluable assistance in criticizing the preparation of the manuscript. The further help of Dr. A. G. Vestal, Dr. W. B. Davis and Dr. D. F. Hoffmeister in reading the manuscript and suggesting certain alterations is gratefully acknowledged. As it was impossible to recheck conditions in the field at the time of writing, any taxonomic or ecological errors remaining must be attributed to the faulty notes or judgment of the author.

Botanical History

Botanical exploration of the Huachuca Mountains began in the 1880's with the pioneering work of Edward Palmer, M. E. Jones, and J. G. Lemmon. In the 90's Major T. E. Wilcox, then commander of Fort Huachuca, made important plant collections in the area. In 1892-93 E. A. Mearns and F. X. Holzner collected plants in the Huachucas in their work with the Mexican Boundary Survey. In the early part of this century L. N. Goodding worked the Huachucas, continuing intermittently to the present.

While the flora of the Huachuca Mountains is quite well known, very little ecological work has been done there. Shreve (1915) presented a discerning discussion of the vegetation of the Santa Catalina Mountains, much of which is applicable to the Huachucas, although geology and topography and their resulting influences differ considerably in the two ranges. Dice and

[1] Paper based upon information collected under Pittman-Robertson Project 46-R, Arizona Game and Fish Commission.

Blossom (1937) described some animal-plant relationships in a small fraction of the range (Miller Canyon). Dice (1943), in his provisional classification of biotic provinces of North America, includes this region in the Apachian Biotic Province whereas in the former paper it had been considered in the Chihuahuan Province (in the Huachuca Biotic District). A vegetational classification of Cochise County, including the Huachuca Mountains, was prepared by Darrow (1944). Much work remains to be done before significant progress may be made in biotic geography. It is believed that descriptions of restricted areas such as this one are essential to that progress.

GEOLOGY

The Huachuca Mountains are drained largely by the San Pedro River flowing northward out of the State of Sonora to the Gila River. The mountains of the San Pedro Valley region are described as resulting from uplifts involving the Gila conglomerate subsequent to its deposition in the Pliocene, the Gila conglomerate now being valley fill (Bryan, 1926). This picture is somewhat complicated by the contention that the Huachuca Mountains were never completely covered by the Gila conglomerate but show evidence of having been a source of supply to this formation (Alexis, 1949).

The Huachuca Mountains are generally quite precipitous, rising at points on the east side from 5000 feet to 9445 feet in three horizontal miles. They consist essentially of a single southeast-northwest ridge, although secondary faulting and folding, plus the dissection of erosion, greatly modify this configuration. There are four prominent peaks, Miller (9445 feet), Carr (9214), Ramsay (8751) and Huachuca (8406) in that sequence from southeast to northwest. A low pass, 6500 feet, between Ramsay and Huachuca peaks gives the appearance of dividing the range into two parts.

Several geologic formations now exposed greatly influence plant cover. Most of the lower eastern slopes of the range are granite of Pre-Cambrian origin. The meeting of the pediment gravels and this granite demarks the Basin and Range Fault. Expressed most simply, the eastern side of the range consists of a broad belt of granite foothills overlaid by more or less steep quartzite cliffs. The quartzite is capped by limestone several hundred to over a thousand feet in total thickness which constitutes the higher elevations in the northern part of the range.

The west side of the range is more difficult to present so schematically, because it is greatly complicated by folding. It is composed largely of calcareous clastics. There is little volcanic rock except to the west in areas which are not covered in this paper.

Available information on soil character as related to plant distribution is so limited that such correlations are avoided in this presentation. Apparently the soil zonation conforms with that of the Graham Mountains described by Martin and Fletcher (1943). There the desert-scrub zone, below 3600 feet, is on red desert soils; the desert grassland, 3000-5000 feet, on reddish-brown soils; the oak woodland, 4800-6000 feet, on shantung brown soils; forest types above oak woodland, 5800 feet and over, are on gray-brown podzols.

The geological term *pediment* is synonymous with the term *bajada* used by plant ecologists to describe the outwash plains of the desert mountain ranges. The term bajada is used hereafter in discussing vegetal situations.

CLIMATE AND PLANT GROWTH.

Rainfall in southeastern Arizona comes principally in two seasons, December through February and July through September, the latter ordinarily accounting for over half the annual precipitation. The driest period is April to June. At Fort Huachuca an average of 17.3 inches has been recorded for a 20-year period (U.S.D.A., 1941). This is not representative of all points of the range because of the variation with elevation. Nearby Fairbank, Arizona, approximately 1000 feet lower than the Fort Huachuca station averaged 12.06 inches for a 29-year period. At the highest elevations precipitation probably exceeds 30 inches.

From May to September temperatures exceeding 100°F may occasionally be expected. In that season the days are usually hot and the nights cool. The record high is 105°F. Below-freezing temperatures are common throughout the winter; the record low is 0°F. A July average of 76.6°F and January average of 45.9°F are computed for Fort Huachuca.

The climate of the low elevations is obviously consistent with and responsible for a Lower Sonoran flora. But periodic fluctuations in this climate result in the lowlands being in a tension zone between desert grassland and desert scrub. Some authors (Weaver and Clements, 1938; Whitefield and Beutner, 1938) hold that desert scrub found in this area is disclimax desert grassland, although the basis for that belief seems rather inconclusive. Brown (1950) and Humphrey (1953) believe that desert grassland in southern Arizona is subclimax to a climax of shrubs and low trees.

The conditions of relative aridity and warmth in recent years seem inconsistent with the presence of coniferous forest at higher elevations, but it is apparent that this has not always been the case. Streamflow in 1877 and 1879 was far greater than it is now, judging from early records (Lage, 1949). Mearns (1907) mentions fish in Tanner's Canyon (Garden Canyon) in 1893, a stream that now contains no fish and, in fact, was dry for virtually its entire length in the summer of 1951. Swarth (1904) tells of 8 feet of snow on the divide in February, 1903. The winter of 1948-49 was cold and several feet of snow accumulated at the higher elevations. The larger streams ran continuously through 1949.

The common assertion that southern Arizona has experienced relative drought for two decades or more is difficult to substantiate with long-term weather records. Annual and short-term climatic fluctuations in the Southwest are extreme but there seems to be little evidence for long-term or progressive climatic changes during the last 2000 years (Thornthwaite, Sharpe and Dosch, 1942). It is apparent that there has in the past been a tendency for Douglas fir, as an example, to spread down certain of the canyons. But present appearances indicate that they have been receding for several years as the lower trees die out, which may or may not be a reflection of climate. At any rate, where climatic variations are extreme ecotones must be considered highly dynamic.

The growing season at Fort Huachuca, as averaged by climatologists, is 232 days, but for the native vegetation there are really two seasons of growth determined by the seasons of precipitation. The lesser one is in early spring following the winter rains and rising spring temperatures. The major one

occurs during the summer rainy season. The entire ecology is adjusted to this summer rainfall. It is the season that produces the bulk of the grazing forage. The perennial grasses of the plains make their greatest vegetative growth and mature in late summer.

Spring is the critical period for grazing because the *carry-over* plants are dependent upon the undependable late-winter rains. Annual herbs become more apparent at this season. If the late-winter rains fail, there is a dearth of green vegetation until summer. It is apparent, and important to mention, that the reduction of ground cover through over-grazing of the desert grassland increases evaporation and early soil drying so that the critical nature of this period is intensified. The results are important to the livestock economy and to wildlife through the influence on ecological conditions which have maintained a grassland vegetation.

VEGETATION

The ecology of an area of topographic extremes is very complex. Precipitation varies with elevation; evaporation varies with slope and exposure; insolation varies with elevation and slope in relation to the direction of light. These conditions give rise to a great variety of habitats, or ecological niches, which make possible a larger number of life forms than could occur in an equal area of uniform topography. In general, on the mountains of southeastern Arizona there exists an upward transition from desert vegetation to coniferous forest, as diagrammed by Shreve (1915). On southern exposures corresponding zones are theoretically higher than they are on northern slopes.

While other factors, mainly geologic, greatly alter this schematic situation, it explains quite well the broad vegetation zones of the Huachuca Mountains. The San Pedro Valley, with an elevation of some 4000 feet, has a desert scrub flora. Higher on the bajada, roughly at 4500 feet, true desert grassland begins and continues to the foothills at about 5000 feet where chaparral or oak woodland takes over. Forests dominated by coniferous trees occur mainly above 7000 feet.

Three major zonal categories used in this discussion are 1) desert scrub and grassland, 2) encinal, and 3) forest. These correspond roughly to the Lower Sonoran, Upper Sonoran and Transition Life Zones of Merriam. Despite the widespread acceptance of Merriam's classification, its several undesirable implications led to the use of other terminology in this report. The map shows the vegetation types according to the classification given below.

Both scientific and common names of plants are given on first mention of the plant, but on subsequent mention only the common name is used in most cases. The nomenclature of Kearney and Peebles (1951) is followed throughout. The term forbs is used in its common definition as applying to dicotyledonous herbs.

DESERT SCRUB AND GRASSLAND ZONE (BELOW 5000 FEET)

Desert Scrub.—Desert scrub occurs primarily below 4500 feet in this area and consequently is very limited in this discussion. In the area covered by the map (fig. 1) this zone is found only as alternes along lower washes in the desert grassland. The dominant plant is whitethorn (*Acacia constricta*). Creosotebush (*Larrea tridentata*) is somewhat less common, becoming more

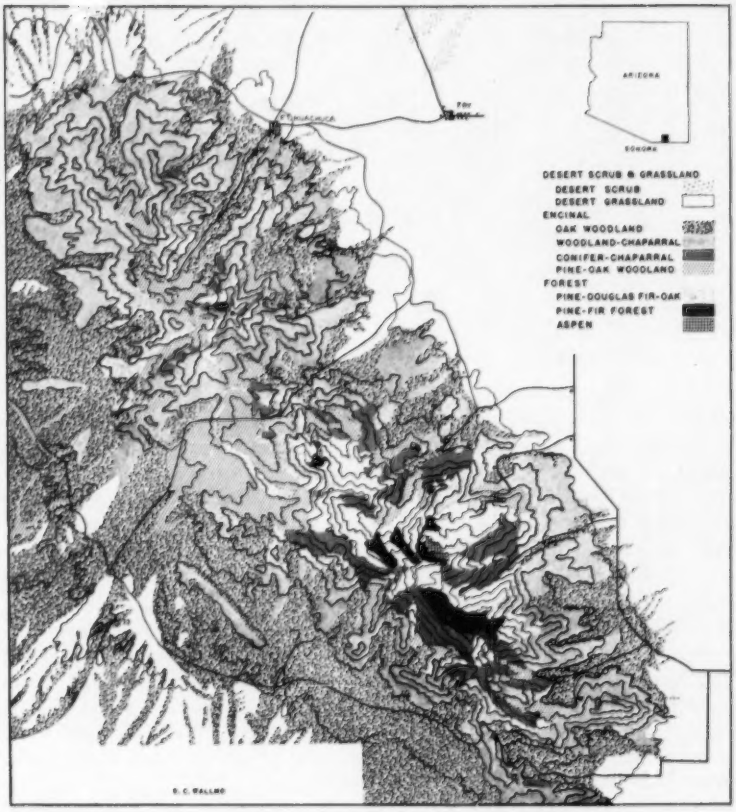


FIG. 1—Vegetation types of the Huachuca Mountains.

abundant at lower elevations. There are occasional mesquites (*Prosopis juliflora*) especially in the wash bottoms, yuccas (*Yucca elata*), and Mexican-tea (*Ephedra trifurca*). The principal grasses are black grama (*Bouteloua eriopoda*), crowfoot grama (*Bouteloua rothrockii*), burrograss (Scleropogon brevifolius), fluffgrass (*Tridens pulchellus*), hoegrass (*Muhlenbergia porteri*), and three-awns (*Aristida* spp.). Desertholly (*Perezia nana*) and burroweed (*Aplopappus tenuisectus*) are common weeds.

Grasses are for the most part very sparse in the desert scrub. Soils are mostly reddish brown at the surface, gravelly and well-drained except in flats where there has been greater accumulation of fine materials and better development of the caliche layer. Such areas are typified by tobosa grass (*Hilaria mutica*). Apparently there has been a great loss of grasses in recent decades accountable to heavy grazing, under which grasses have been unable to withstand both excessive cropping and severe moisture competition. Hoegrass, blackgrama and crowfoot grama, the earlier dominants, are now secondary to

fluffgrass, burrograss and three-awns, which are better able to make use of the brief periods of moisture.

Desert Grassland.—There is a very marked elevational zonation of grassland subtypes in the narrow gradient of some 500 to 600 feet elevation between the desert scrub and the foot of the mountain. Considering the desert grassland schematically as an undissected bajada, the transition is from black grama domination to blue grama domination, then to a complex of higher-elevation communities at the base of the mountain, variously dominated by plains lovegrass (*Eragrostis intermedia*), curly mesquite (*Hilaria belangeri*), slender, hairy, spruce-top and side-oats grama (*Bouteloua filiformis, B. hirsuta, B. chrondrosioides, B. curtipendula*) and others.

The lowest belt, black grama, may be considered ideally as a consociation. Where it has not been excessively grazed, black grama is the single dominant. On heavily grazed areas and on poorer sites, annual burroweed (*Aplopappus gracilis*), stickystem (*Boerhaavia coccinea*), showy goldeneye (*Viguiera multiflora*), croton (*Croton corymbulosus*), zinnia and other weeds are as conspicuous in the sparse aspect as black grama. Several composition estimates in the black grama subtype (on lightly grazed range) showed black grama to compose about 26 percent of the cover, the remaining 74 percent being variously divided among blue, sideoats and other gramas, plains lovegrass, beardgrass (*Andropogon barbinodis*), curly mesquite, vine mesquite (*Panicum obtusum*), tobosa, fluffgrass, false mesquite (*Calliandra eriophylla*), mesquitilla (*Calliandra humilis*), Wright's buckwheat (*Eriogonum wrightii*), Mexican-tea, yellow ragweed (*Bahia absinthifolia*), and the weeds mentioned above.

The soaptree yucca (*Yucca elata*) is often a conspicuous member of this community. While not so evident immediately around the Huachucas, in nearby areas its invasion and spread appears to be accelerated by disturbance through livestock use. Pricklypear and other cacti are common in the black grama belt along with false mesquite and purslane (*Portulaca* sp.). Ocotillo (*Fouquieria splendens*) occurs in limited stands usually on calcareous outcrops.

As elevation increases the grassland changes from black-grama domination to blue-grama domination with a belt about one mile in width, varying with the slope of the bajada (narrower on steeper pediments), where they may be considered codominants. In this range there are no true subdominants but in restricted situations societies of other species are more manifest than black and blue grama. Examples are swales of vine mesquite, washes of sacaton (*Sporobolus wrightii*), and draws with sideoats, beardgrass, sand dropseed (*Sporobolus cryptandrus*) and other coarse grasses of higher moisture requirements.

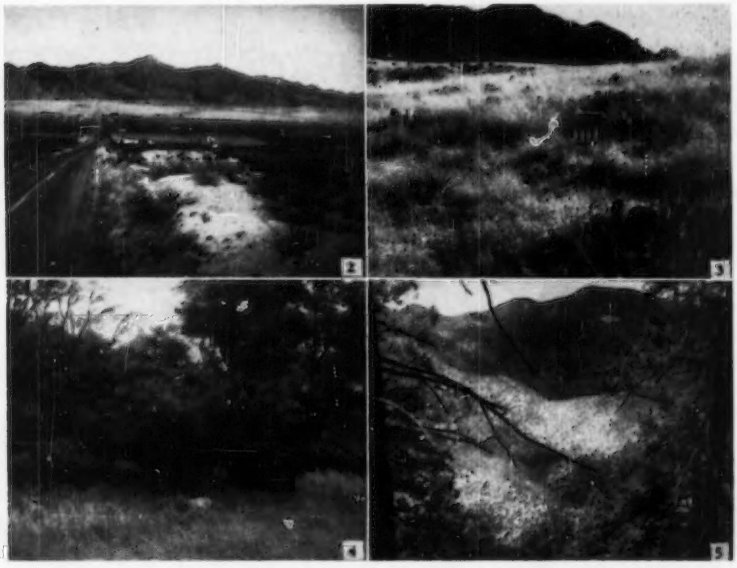
Gradually black grama disappears and blue grama becomes the single dominant at elevations of 4700 feet. The blue grama consociation is best developed on broad level bajadas with relatively fine soils. Where the bajada is dissected by washes it is replaced by coarser grasses adapted to rockier slope and ridge sites, such as beardgrass, pappusgrass (*Enneapogon devauxii*), sideoats, sprangletop (*Leptochloa dubia*) and crinkleawn (*Trachypogon secundus*). Washes with broad bottoms that are not completely occupied by water channel are usually occupied by blue grama in this belt.

On sites in better condition, particularly within the Fort Huachuca Military Reservation, blue grama comprises upward of 50 percent of the total plant

density, with density itself exceeding a 50 percent cover. On very poor sites it may make up only 5 percent and yet remain the dominant component over annual three-awn (*Aristida adscensionis*), Arizona three-awn (*A. arizonica*), red three-awn (*A. longiseta*), spidergrass (*A. ternipes*), poverty three-awn (*A. divaricata*), Arizona muhly (*Muhlenbergia arizonica*), bristlegrass (*Setaria* sp.), peppergrass (*Lepidium thurberi*), sorrel buckwheat (*Eriogonum polycladon*), and many other weeds.

Mesquite is an aggressive invader into the blue grama consociation, resulting in areas which might be placed in what other authors have called a mesquite-grassland association. However, that terminology is misleading. While mesquite apparently invades both good-condition and poor-condition ranges, here it is most extensive on areas with histories of heavier grazing use. In some areas, especially on grasslands east of the mountains, groundsel (*Senecio longilobus*) and burroweed are abundant invaders. Broomweed (*Baccharis thesioides*) is often common along with mesquite, usually associated with more extreme disturbance.

Relative to the assertions of Whitfield and Beutner (1938) that all of the desert scrub in this region is climax desert grassland reduced to a disclimax condition, it is notable that creosotebush has invaded—if it has done that—only below certain levels. In the blue grama range, mesquite is the only widespread shrub invader. It is apparent that the higher grassland ranges are



FIGS. 2-5.—2. View of Huachuca Mountains from the East, looking across San Pedro Valley; 3. Desert grassland at 5100 feet elevation composed mainly of curly mesquite and mixed gramas; 4. Oak woodland at 5500 feet in canyon bottom, with grassy openings of sideoats and blue grama; 5. Conifer forest on north slope at 7800 feet, with chaparral on south slopes of Huachuca Peak in background.

more resistant to shrub invasion, but it is also apparent that over-grazing can defeat this resistance. The role of fire in controlling shrub invasion is a matter of great interest (Humphrey, 1949, 1953).

Sporadic natural fires are assumed to be responsible for the maintenance of the original grasslands. Also, good grass stands were apparently necessary for the occurrence of effective fires. Thus, while an academic question stands as to what is climax, the fire problem is of great practical interest in range management research.

Colloquially the broader ridges between washes on the bajadas are called mesas. At elevations approaching or slightly exceeding 5000 feet on these so-called mesas, domination is taken over by plains lovegrass with the following species included among the secondary grasses: hairy, blue, slender, purple and spruce-top gramas, crinkle-awn, several perennial three-awns (e.g., *Aristida ternipes, A. arizonica, A. longiseta*), purple muhly (*Muhlenbergia rigida*). Texas timothy (*Lycurus phleoides*), and beardgrass. In the same elevational range, curly mesquite, a close-growing, high-quality grass (for forage and erosion control), dominates large areas, particularly rocky slopes and ridges (fig. 2).

Passing up the slopes into the chaparral and woodland types the species listed continue but are gradually replaced by other species, notably bullgrass (*Muhlenbergia emersleyi*), *M. longiligula,* beggartick grass (*Aristida orcuttiana*), Texas beardgrass (*Andropogon cirratus*), and woolly bunchgrass (*Elyonurus barbiculmis*).

Cliffrose (*Cowania mexicana*) which, elsewhere, is usually found in the piñon-juniper association, or in similar woodland or chaparral types, is found in this area in colonies in the grassland belt on limestone or clastic outcrops, either on the ridges or in washes which cut through the pediment gravels into those underlying formations. Apache plume (*Fallugia paradoxa*) is limited to a small stand within the grassland belt beside the walnut-desertwillow-lined course of Huachuca Canyon. Common trees and shrubs along washes in the grassland belt are desertwillow (*Chilopsis linearis*), walnut (*Juglans major*), ash (*Fraxinus velutina*), desert hackberry (*Celtis reticulata*), cottonwood (*Populus fremontii*), and sycamore (*Platanus wrightii*).

In some parts of the upper grasslands there are extensive dense stands of mescal (*Agave parryi*) occupying ridge and slope sites. Oftentimes they are mixed with pricklypear (principally *Opuntia engelmannii*) and sotol (*Dasylirion wheeleri*). The yewleaf willow (*Salix taxifolia*) lines a few of the washes on the north end of the mountains where there is a fairly dependable supply of non-capillary groundwater. Deergrass (*Muhlenbergia rigens*) also characterizes some of the washes in the grassland with some underground seepage. It also continues up the canyons into the woodland for some distance.

ENCINAL ZONE (ABOVE 5000 FEET)

The genus *Quercus* is the dominant single genus of trees in the Huachuca Mountains, permitting the application of the term encinal (*encina* = evergreen oak, Spanish) to much of the wooded area. In this treatment we break the encinal into two types: oak woodland and chaparral. The Encinal Zone is also credited with a pine-oak woodland type and a chaparral-conifer type.

Oak Woodland.—At elevations slightly below 5000 feet, along the wash

bottoms on the bajadas, the oaks make their first appearance. The lowest form in elevation is Mexican blue oak (*Quercus oblongifolia*). It is soon joined by Emory oak (*Q. emoryi*), then by Arizona white oak (*Q. arizonica*). These three often occur together, but *Q. oblongifolia* is seldom found above 5200 feet. Approximately at 5200 feet silverleaf oak (*Q. hypoleucoides*) appears. Emory, Arizona, and silverleaf oaks are found in mixtures in the lower reaches of the mountain canyons.

The oak woodland is best developed in the canyons and on lower northerly slopes (fig. 4). It forms an open savanna in many places along the foot of the mountains at the heads of the bajadas. On the west side of the mountains oak woodland occupies a belt on the bajada one to three miles wide. This is discussed later. Farther up the canyons and on the lower northerly slopes the trees become more dense, with Emory, Arizona and silverleaf oaks still dominant. Higher up, netleaf oak (*Quercus reticulata*) and Gambel oak (*Q. gambelii*) are common. They appear first at about 6500 and 7000 feet, respectively. Toumey oak (*Q. toumeyi*), Palmer oak (*Q. palmeri*) and scrub oak (*Q. pungens*) are found in the Huachucas but are very limited in distribution. Palmer oak seems to occur principally in cool sites on or just below the Bolsa quartzite formation.

Alligator juniper (*Juniperus deppeana*) is the most common and uniformly distributed associate of oaks throughout the oak woodland. In the broad woodland belt on the southwest side of the mountains juniper appears to behave differently from the oaks in relation to grazing. Certain areas of grassland at about 5500 feet elevation are being invaded by juniper presumably in response to disturbance of the soil and scarification of seed in the digestive tracts of cattle.

A number of other shrubs and trees occur in the oak woodland. Manzanita (*Arctostaphylos pungens*), silktassel (*Garrya wrightii*), madrone (*Arbutus arizonica*), squawbush (*Rhus trilobata*), Mearns sumac (*R. choriophylla*), and piñon (*Pinus cembroides*) are variously abundant in the higher woodland. In canyon bottoms the magnificent Arizona sycamore is the most striking tree. Cottonwood, willows (*Salix gooddingii, S. exigua,* and others), bigtooth maple (*Acer grandidentatum*) and wild grape also characterize the canyons. At higher elevations pines begin to occur and the oak woodland blends into the pine-oak woodland described below.

To give a clearer description of the elevational transition of species composition the situation in Miller Canyon presented in table 1 and fig. 6 should be reviewed. This canyon is relatively steep and straight, falling in a northeasterly direction. The grassland-woodland ecotone is abrupt at the 5000 foot level. At representative locations along the canyon, approximately at 250 foot elevational intervals, a listing was made of the most conspicuous species in these categories: trees and large shrubs; small shrubs and herbs; grasses.

The altitudinal relations of the pines and oaks of the Huachuca Mountains, along with other major trees, are diagrammed in fig. 7.

As mentioned earlier, the base of the mountain is approximately 1000 feet higher on the west side than on the east. Correspondingly, the upper bajada is in oak woodland on the west side and in desert grassland on the east. It is difficult to find any explanation other than elevation for that fact. The mountain range lies in a southeast-northwest direction parallel to the path of most

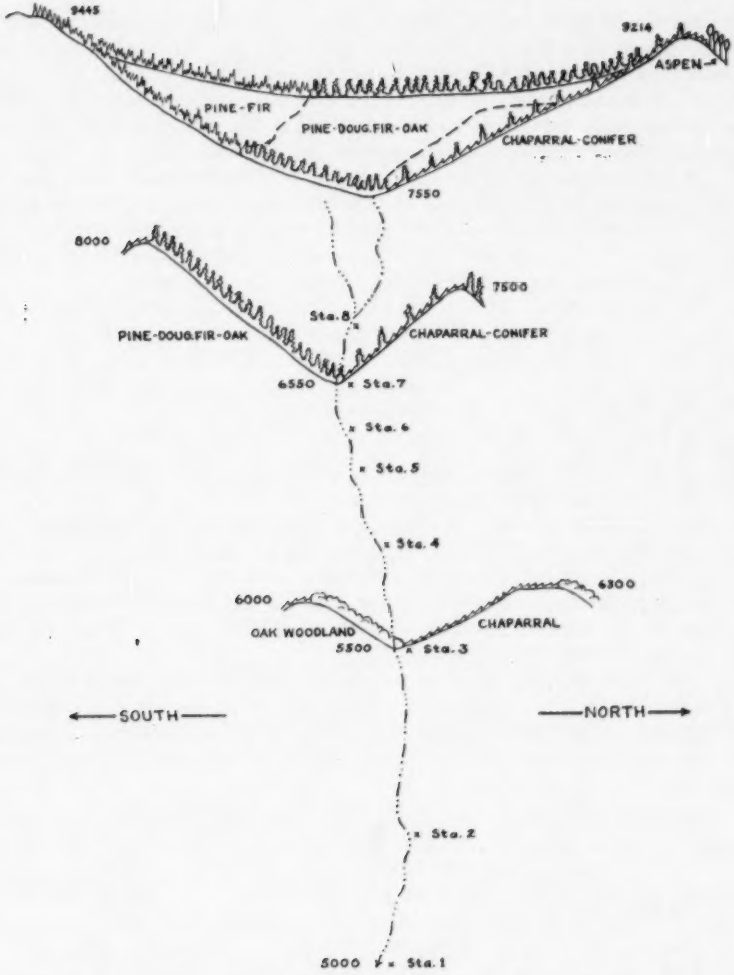


FIG. 6.—Diagram of alterns in Miller Canyon. Stations corresponding to table I are indicated.

of the rainstorms. Thus neither side receives an advantage of precipitation. The west side is much more exposed, which fact, if of any influence, would elevate the more mesophytic situation; that is, woodland. Fig. 8 presents diagrammatically the relative elevation of vegetation zones on the mountain from east to west.

Woodland Chaparral.—In the encinal much of the area—on more exposed sites—is too xeric for the development of large trees. The same oaks that become large trees in the true woodland remain dwarfed here, often forming a

shinnery. Alligator juniper, likewise dwarfed, is usually abundantly distributed among the oaks. On the lower granitic slopes, which characterize the entire eastern base of the mountain, manzanita is most abundant, although it is also found variously common in most sites up to 8000 feet. In certain areas, especially on some exposed ridges, manzanita forms a dense, impenetrable chaparral virtually excluding other trees and shrubs.

Hairy mountain-mahogany (*Cercocarpus breviflorus*) occurs in its greatest abundance and best development on limestone slopes. For example, the entire southeast slope of Huachuca Peak supports a nearly pure stand of mountain-mahogany. Netleaf oak also occurs in dense chaparral (or shinnery) form on some higher sites, the head of Copper Canyon being an example.

For the most part, what is here called woodland chaparral contains a diverse shrub mixture of the previously mentioned oaks along with manzanita, mountain-mahogany, silktassel, Mearns sumac, squawbush, some buckbrush (*Ceanothus fendleri*), and numerous others. In the areas so designated on the map there may be few to many tree-size plants (especially oaks, piñon and juniper) but these areas still have the general character of chaparral.

Chaparral with Conifers.—This designation is applied to higher chaparral stands, usually composed largely of netleaf and silverleaf oak, occasionally of buckbrush or Gambel oak. On these sites conditions seem to be marginal for some of the pines and Douglas fir (*Pseudotsuga taxifolia*). There may be young trees or old fire-scarred relics, possibly indicating that conifers once established there had been wiped out by fire. While these areas may not be significantly different from other chaparral areas they more probably indicate a seral stage toward conifer forest.

The successional status of, especially, the high-elevation, dence chaparral areas is not adequately understood. Many of the stands of manzanita, buckbrush, and of oak shinnery have the appearance of fire disclimax. Evidence in the form of charred remains is available but it can also be found almost everywhere on the mountain.

Pine-Oak Woodland.—At elevations between 5500 and 7500 feet there may be sufficient pines in the woodland to give it an entirely different aspect. Chihuahua pine (*Pinus chihuahuhana*) is found at the lowest elevations mixed in with Emory, Arizona, silverleaf and netleaf oaks. The first two of these oaks drop out with increasing elevation, Emory at about 7000 feet (maximum) and Arizona white oak around 7600 to 8000 feet. Apache pine (*P. latifolia*) enters the association at low elevations, but usually somewhat higher than Chihuahuha pine. At higher elevations ponderosa pine (*P. ponderosa*) may also be found in the pine-oak woodland. Most of the pine-oak woodland is composed largely of silverleaf, netleaf and Arizona white oaks, and Chihuahua, Apache and ponderosa pines. Mexican white pine or limber pine (*Pinus flexilis*), Douglas fir, ash, maple, sycamore, madrone, juniper, piñon, and others are significant members of various faciations.

Canyon-bottom components are much the same as in the oak woodland. Arizona cypress (*Cupressus arizonica*), which occurs in the Chiricahua Mountains to the east and the Santa Rita Mountains to the northwest in canyons in the oak woodland and pine-oak woodland zones, is not found in the Huachuca Mountains.

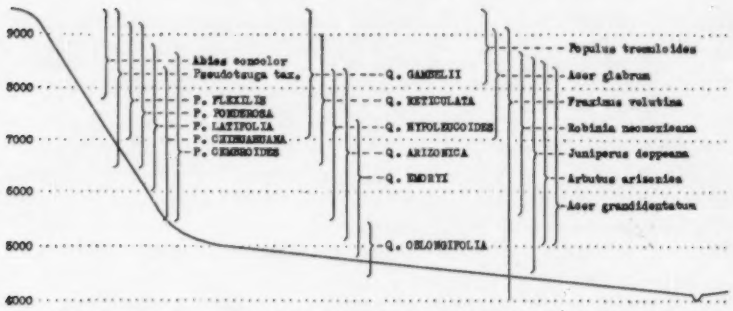


FIG. 7.—Elevation ranges of major trees of the Huachuca Mountains. The dominant genera, pines and oaks, are in capital letters.

Pine-oak woodland is mainly restricted to areas above 5500 feet in the mountains proper. There is an isolated area of pine-oak woodland to the west of the mountain, however, at and below 5500 feet. These trees occur on the edge of the volcanic formation and undoubtedly an edaphic factor is involved.

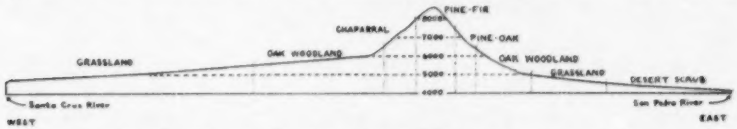


FIG. 8.—Relative elevation of vegetation zones on west (left) and east side of the Huachuca Mountains.

TABLE 1.—Change of composition with increasing elevation, Miller Canyon.

	MAJOR COMPONENTS		
	Trees & Tall Shrubs	Low Shrubs & Herbs	Grasses
Station 1 5000 feet		*Eriogonum wrightii* *Senecio longilobus* *Cassia leptocarpa*	*Eragrostis intermedia* *Bouteloua curtipendula* *B. hirsuta* *B. gracilis* *Aristida orcuttiana* *Andropogon barbinodis*
Station 2 5250 feet	*Arctostaphylos pungens* *Quercus emoryi* *Q. arizonica* *Agave parryi* *Juglans major* *Platanus wrightii*	*Eriogonum wrightii* *Notholaena* sp. *Gnaphalium wrightii* *Vitis arizonica*	*Eragrostis intermedia* *Aristida orcuttiana* *Bouteloua curtipendula* *Andropogon cirratus*
Station 3 5500 feet	*Quercus emoryi* *Q. arizonica* *Arctostaphylos pungens* *Agave parryi* *Juniperus deppeana* *Cercocarpus breviflorus* *Platanus wrightii* *Juglans major*	*Gnaphalium wrightii*	*Eragrostis intermedia* *Aristida orcuttiana* *Andropogon cirratus* *Bouteloua curtipendula* *B. gracilis* *B. hirsuta* *Lycurus phleoides* *Muhlenbergia emersleyi*

Station 4	*Quercus emoryi*	*Gnaphalium wrightii*	*Eragrostis intermedia*
5750 feet	*Q. arizonica*	*Artemisia ludoviciana*	*Aristida orcuttiana*
	Q. hypoleucoides	*Brickellia* sp.	*Muhlenbergia emersleyi*
	Arctostaphylos pungens		*Andropogon cirratus*
	Pinus chihuahuana		
	P. cembroides		
	Juniperus deppeana		
	Agave palmeri		
	Arbutus arizonica		
	Platanus wrightii		
	Juglans major		
	Pseudotsuga taxifolia		
	Cercocarpus breviflorus		
Station 5	*Quercus arizonica*	*Rhus trilobata*	*Muhlenbergia emersleyi*
6000 feet	*Q. hypoleucoides*	*Brickellia* sp.	*Eragrostis intermedia*
	Q. emoryi	*Gnaphalium wrightii*	*Andropogon cirratus*
	Arbutus arizonica	*Ceanothus fendleri*	*Aristida orcuttiana*
	Pinus chihuahuana		
	P. cembroides		
	Pseudotsuga taxifolia		
	Arctostaphylos pungens		
	Juniperus deppeana		
	Acer grandidentatum		
	Juglans major		
	Platanus wrightii		
	Yucca baccata		
Station 6	*Quercus hypoleucoides*	*Gnaphalium wrightii*	*Muhlenbergia longiligula*
6250 feet	*Q. arizonica*	*Philadelphus microphyllus*	*Bromus* sp.
	Acer grandidentatum	*Vitis arizonica*	*Elymus canadensis*
	Pinus ponderosa		
	P. latifolia		
	P. flexilis		
	P. cembroides		
	Pseudotsuga taxifolia		
	Platanus wrightii		
	Juglans major		
	Arbutus arizonica		
Station 7	*Pseudotsuga taxifolia*		*Bromus* sp.
6500 feet	*Acer grandidentatum*		*Muhlenbergia longiligula*
	Pinus latifolia		*M. emersleyi*
	Quercus hypoleucoides		*Elymus canadensis*
	Q. reticulata		
	Juniperus deppeana		
	Arbutus arizonica		
Station 8	*Pseudotsuga taxifolia*	*Symphoricarpos oreophilus*	*Muhlenbergia longiligula*
6750 feet	*Acer grandidentatum*		*Bromus* sp.
	Quercus gambelii		*Elymus canadensis*
	Q. hypoleucoides		*Stipa pringlei*
	Q. reticulata		
	Robinia neomexicana		
	Pinus latifolia		
	P. flexilis		
	Arbutus arizonica		
	Garrya wrightii		
	Yucca baccata		

Shreve's statement that vegetation zones are higher on volcanics is probably an over-generalization (Shreve, 1922).

FOREST ZONE (ABOVE 7000 FEET).

Pine-Douglas Fir-Oak.—Pine-oak woodland is found principally on relatively xeric sites. On more favorable sites, that is, northerly slopes or sheltered canyons, the woodland may blend from pine-oak woodland, or directly from oak woodland into a forest of pines, Douglas fir and more mesophytic oaks. That transition occurs sometimes as low as 6500 feet but usually above 7000 feet. The type is separated from pine-oak woodland on the basis of more mesic components. It has the general aspect of conifer forest rather than of xeric woodland.

The most abundant trees are Douglas fir, Mexican white pine (limber pine), and Arizona pine (ponderosa pine), followed by Gambel oak, maple (mostly *Acer glabrum*), ash and New Mexican locust (*Robinia neomexicana*). There is no upper elevational limit for the type but on cooler high sites the next two types replace it. In the pine-Douglas fir-oak belt, snow often remains on the ground for three or more months in the winter.

Many chaparral and woodland elements may occur in the community but they are always limited. As a result of the dissected nature of the mountains each mountainside is covered with a complex mixture of alternes rather than with distinct elevational zones of vegetation. One may step, literally in a few steps, from conifer forest into a cactus garden (*Mammillaria* sp., *Opuntia* sp.), into a yucca or an agave stand, or into xeric woodland or chaparral.

Pine-Fir Forest.—The highest vegetational zone in the Huachuca Mountains is characterized by white fir (*Abies concolor*), Douglas fir, several pines, and aspen (*Populus tremuloides*). This belt is mainly restricted to the cool north and northeast exposures of Miller Peak and Carr Peak from the summits (9445 and 9214 feet) down to about 7500 feet. Smaller areas occur on the north faces of Ramsay Peak (8751 feet) and Huachuca Peak (8406 feet) down to about 8000 feet.

It has been noted before (Shreve, 1915) that the total bulk and height of the desert mountain ranges has an influence on the elevational levels of the respective vegetation types. For example, the Mule Mountains with a maximum elevation of 7800 feet have no true conifer forest, while the Huachuca Mountains have conifer forest extending as low as 6000 feet. The Chiricahua Mountains, reaching 9795 feet and having much greater total bulk, have Engelmann spruce (*Picea engelmanni*) well below 9000 feet while the Huachucas reaching 9445 feet have no Engelmann spruce. The generalization may be made for this region that the larger the mountain is the lower the more mesic communities will grow. This contradicts the principle as stated elsewhere (Daubenmire, 1947).

In earlier days considerable logging was carried on in the conifer forests of the Huachucas, mainly on "the Reef," a less precipitous area above the quartzite cliffs and below Carr Peak. Extensive logging was also done below Ramsay Peak on the military reservation. A devastating fire near the turn of the century terminated logging in the Reef area and no commercial operations have since been conducted. Mexican white pine (*Pinus flexilis*), Arizona pine (*P. ponderosa*), Apache pine and Douglas fir were the major timber species.

Aspen.—Forests of quaking aspen occur only on the highest and coolest sites in the Huachuca Mountains. The largest of such stands is found on the northeast face of Carr Peak. There are smaller areas on the northwest side of Carr Peak (head of Ramsay Canyon) and the north face of Miller Peak but they are so limited that they are not shown separately on the map.

Dense growths of fire willow, referred to *Salix scouleriana* by Goodding (personal communication), are found mixed through the aspen. The extensive stands of aspen along with fire willow may be considered here, as elsewhere, as a result of fire, and may be expected to develop eventually into fir forest. The fact that only the coolest sites bear aspen forests may indicate that their seral development is toward a more mesic climax than the pine-fir forest discussed above; that is, to a conifer forest more clearly dominated by white fir. In discussing the avifauna of the nearby Santa Rita Mountains, Bailey (1923) considers aspen forests in the Canadian Life Zone which would perhaps place them zonally above the present classification.

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The Taxonomy of the North American Acaulescent White Violets

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The small, stemless, white-flowered violets of North America have long presented problems in identification to American taxonomists. They have never been studied as a group, though Brainerd (1905) discussed the eastern forms, and Gershoy and his associates (Gershoy, 1928, 1934; Bamford and Gershoy, 1930) have worked with all of them in their cytological studies. They are treated here as six species, belonging to the Section Nominium, Subsection Plagiostigma, Group Stolonosae, of the Genus *Viola*. In addition to the six white-flowered violets, the Group Stolonosae includes two circumpolar, blue-flowered species, *V. palustris* L. and *V. epipsila* Led., which are not dealt with here. The scheme of classification used above is taken from the works of Bamford and Gershoy (1930) and Gershoy (1934). These authors further break the Group Stolonosae into three subgroups: the subgroup Primulifoliae, including *V. lanceolata, V. primulifolia, V. macloskeyi* and *V. renifolia,* the subgroup Blandae, including *V. blanda* and *V. incognita,* and the subgroup Palustres, composed of *V. palustris* and *V. epipsila.* From all available evidence, this seems to be a natural grouping. In addition to morphological evidence, to be later discussed, the first two subgroups are separated by chromosome number and, though fertile hybrids are produced within each subgroup, only sterile hybrids are produced in intergroup crosses (Bamford & Gershoy, 1930). The subgroup Primulifoliae has a diploid chromosome number of 24 (Gershoy, 1934), while the subgroup Blandae is characterized by a diploid chromosome number of 48 (Clausen, 1929).

The present studies were made during 1948, 1949 and 1950. This is the introductory paper in a series to be presented upon variation in the stemless white violets. Some of the evidence for the decisions rendered here must be presented in summarized form in this paper and will be dealt with in detail in later papers.

Acknowledgements.—I wish to express my appreciation to Dr. Gerald B. Ownbey of the University of Minnesota for his very helpful assistance in many phases of the investigation, to Mr. C. C. Deam of Bluffton, Indiana (DEAM), and to the curators of the Herbaria at the institutions given below for the loan of herbarium specimens: Gray Herbarium of Harvard University (G), New York Botanical Garden (NY), United States National Herbarium (US) Missouri Botanical Garden (MO), University of California for both their collections (UC) and for material from the Clokey Herbarium (CLOKEY), University of Georgia (GA), University of Pennsylvania (UP), University of Indiana (IND), University of Wisconsin (WIS), University of Tennessee (TENN), State University of Iowa (IOWA), University of Minnesota (MINN), Ohio State University (OHIO), Washington State College (WS), Oregon State College (OS), and North Dakota Agricultural College (ND). The cited specimens were chosen and are representative, though they represent only a portion of the number examined.

In addition to specimens from the herbaria mentioned, I have used personal collec-

tion. In all about 5000 specimens were examined. I am also indebted to the Chicago Natural History Museum for the loan of photographs of the type specimens of *Viola lanceolata* L. and *V. primulifolia* L.

KEYS TO THE SPECIES

Both spring and summer keys are provided, since the salient characters of the species differ at the two seasons. In the spring some flower characters and in the summer certain capsule characters are necessary for proper determination.

SPRING KEY TO THE STEMLESS WHITE VIOLETS

A. Leaves longer than broad, varying from ovate to linear, the bases cuneate or occasionally truncate and rarely slightly cordate.
  B. Leaves ovate, about 1.5 or 2 times as long as broad.
    C. Petals beardless or with very slight beard; eastern North America.
      D. Leaves glabrous, usually cuneate, though occasionally truncate at the base; eastern and northeastern North America ..... 2. *V. primulifolia* subsp. *primulifolia*
      D. Leaves slightly to very pubescent, with slightly cordate bases; eastern and southeastern United States ..... 2a. *V. primulifolia* subsp. *villosa*
    C. Petals with a dense beard; western United States ..... 1b. *V. lanceolata* subsp. *occidentalis*
  B. Leaves linear to lanceolate, from 3.5 to 15 or more times as long as broad.
    E. Leaves lanceolate, the blade from 3.5 to about 6 times as long as broad; eastern and southeastern United States ..... 1. *V. lanceolata* subsp. *lanceolata*
    E. Leaves linear, the blade from 6 to 15 times as long as broad, especially in late spring and summer; southeastern United States .... 1a. *V. lanceolata* subsp. *vittata*
A. Leaves as broad or broader than long, moderately to broadly ovate; the bases always cordate.
  F. Lower pair of petals always beardless.
    G. Leaves pubescent on the upper surface only, deeply cordate, about as long as broad ..... 5. *V. blanda*
    G. Leaves glabrous or pubescent, but very rarely pubescent on the upper surface only, orbicular, sometimes almost twice as broad as long ..... 4. *V. renifolia*
  F. Lower pair of petals slightly to very pubescent with small, cylindrical, white hairs.
    H. Leaves cordate, from .8 to 1.2 times as long as broad; petals usually with a slight or heavy beard.
      I. Leaves with 8 or more crenations per side (usually about 15), with marked basal lobes; lateral petals beardless or with a scant beard; eastern North America ..... 3a. *V. macloskeyi* subsp. *pallens*
      I. Leaves with 0-4 crenations per side, with very shallow basal lobes; lower pair of petals with a heavy beard; California and Oregon ..... 3. *V. macloskeyi* subsp. *macloskeyi*
    H. Leaves cordate to somewhat reniform, from .65 to .85 times as long as broad; lower pair of petals with moderate to heavy beard; northeastern ..... 6. *V. incognita*

SUMMER KEY TO THE STEMLESS WHITE VIOLETS

A. Cleistogamous capsules green, borne on either erect or spreading peduncles; stolons well developed.
  B. Leaves as broad as or broader than long, the bases always cordate.
    C. Leaves with 8 or more crenations (usually about 15) per side, with marked basal lobes ..... 3a. *V. macloskeyi* subsp. *pallens*
    C. Leaves with typically 0-4 crenations per side, with very shallow basal lobes ..... 3. *V. macloskeyi* subsp. *macloskeyi*
  B. Leaves longer than broad, varying from ovate to linear, the bases cuneate or occasionally truncate and rarely slightly cordate.
    D. Leaves ovate or obovate; about 1.5 or 2 times as long as broad.

E. Leaves ovate; eastern North America.
F. Leaves glabrous, cuneate at the base; eastern and northeastern North America ..... 2. *V. primulifolia* subsp. *primulifolia*
F. Leaves slightly to very pubescent, with truncate or cordate bases; eastern and southeastern United States ..... 2a. *V. primulifolia* subsp. *villosa*
E. Leaves obovate, western North America ..... *V. lanceolata* subsp. *occidentalis*
D. Leaves linear to lanceolate, from 3.5 to 15 or more times as long as broad.
G. Leaves lanceolate, from 3.5 to about 6 times as long as broad; eastern and northeastern North America ..... 1. *V. lanceolata* subsp. *lanceolata*
G. Leaves linear, 6-15 or more times as long as broad; eastern and southeastern United States ..... 1a. *V. lanceolata* subsp. *vittata*
A. Cleistogamous capsules ordinarily purple or purple-spotted, borne on prostrate peduncles; stolons either well-developed or absent.
H. Plants bearing short, fruiting stolons but not vegetative stolons; leaves orbicular, about .65 times as long as broad ..... 4. *V. renifolia*
H. Plants bearing vegetative stolons but not fruiting stolons; leaves cordate, from about .80 to 1.00 times as long as broad.
I. Leaves about as long as broad, the basal sinus small; leaves always pubescent, but only on the upper surface ..... 5. *V. blanda*
I. Leaves from .75 to .85 times as long as broad, the basal sinus large; leaves variously pubescent ..... 6. *V. incognita*

DESCRIPTIONS OF THE SPECIES AND SUBSPECIES

1. VIOLA LANCEOLATA L. subsp. LANCEOLATA

V. lanceolata L., Sp. Pl. 934. 1753, in the restricted sense.

Acaulescent from long, slender, usually prostrate rootstocks; vegetative reproduction by leafy stolons produced as lateral branches which arise from near the apical end of the rhizome and immediately curve downward, ultimately lying horizontally just beneath the duff or on the surface of the ground, later becoming detached and producing new plants from crowns at their tips; plants small, up to about 5 cm high in the spring, becoming 7 to 10 cm high in the summer; rootstocks usually 2-4 mm in diameter near the apex, 1-1.5 mm in diameter farther back, occasionally thicker; peduncles, petioles and leaf blades typically entirely glabrous, but rarely somewhat pubescent on the upper side of the leaves; leaves lanceolate, obscurely crenate-serrate along the apical two-thirds of the margin, gradually tapering basally into a long, narrowly margined petiole; peduncles reddish-purple-specked along the upper half, sometimes along the whole length in young plants, commonly equaling or exceeding the leaves in the spring, shorter than the leaves in the summer and fall; sepals of the petaliferous flowers ovate-lanceolate, scarious-margined, dark green, auricled, with inconspicuous veins; petals white, the lower three, especially the spurred one, deeply veined with dark purple, not bearded, rarely the lower pair of petals with a few hairs; lower pair of petals lanceolate; both cleistogamous and chasmogamous capsules green, glabrous and oval; seeds dark brown to black, 1-1.2 mm long.

V. lanceolata subsp. *lanceolata* is found from Cape Breton west to Minnesota and south to Florida and eastern Texas. In addition it has been reported from Washington by Schultz (1946) and from Venezuela by Baker (1940).

ARKANSAS: Malvern, Hot Springs Co., *Palmer* 29584 (NY). CONNECTICUT: Bridgeport, *Eames* (US, G). DELAWARE: 1 mi. east of Lewes, Sussex Co., McVAUGH 6558 (MO, NY, G). DISTRICT OF COLUMBIA: Washington, *Ward* (US). ILLINOIS: Chicago, Cook Co., *Babcock* (MO); St. Anne, Kankakee Co., *Jones* 11444 (NY); Illinois R., Ottawa, LaSalle Co., *Johnson* (MO, US, G). INDIANA: Lake Cicott, Cass Co., *Deam* 19372 (NY, DEAM); 4 mi. no. of Elkhart, Elkhart Co., *Deam* 53630 (DEAM); 1 mi. no. of Griffith, Lake Co., *Deam* 40506 (DEAM); Mineral Springs, *Lansing* 3365 (US, WIS, G); Miller's, *Umbach* (MO, WIS, NY, US, G). IOWA: Muscatine, Muscatine Co., *Shimek* (WIS, IOWA). KENTUCKY: East Bernstadt, Laurel Co., *McFarland* (GA, MO, NY, DEAM, TENN, G); Mammoth Cave Nat'l. Park, *Lix* 364 (US). MAINE: Chesterville, Franklin Co., *Eaton* (WIS); Monhegan Is., Lincoln Co., *Churchill*

(MO); Brooks, Waldo Co., *Fassett* 3649 (WIS). MARYLAND: Hyattsville, *Dowell* 6466 (NY, MO, G). MASSACHUSETTS: Dennis, Barnstable Co., *Fernald & Long* 17185 (NY); Ludlow, Hampden Co., *Seymour* 551 (NY, MO); Needham, *Churchill* (US, MO); Lake Massapoag, *Greenman* 1673 (MO, G). MICHIGAN: Ludington, Mason Co., *Chaney* 195 (NY); Muskegon State Park, Muskegon Co., *Hermann* 8648 (NY); Pentwater, Oceana Co., *Miller* (TENN, GA); Grand Rapids, Kent Co., *Shaddick* (US, NY, G). MINNESOTA: Anoka, Anoka Co., *Ines* (NY, G, MINN); 11 mi. no. of Minneapolis, Anoka Co., *Rosendahl* 1226 (DEAM, G, MO, MINN, NY). MISSOURI: Between Gladden & Timber, Dent Co., *Palmer & Steyermark* 41412 (MO, NY, TENN); Sect. 4, Oregon Co., *Steyermark* 5372 (Mo). NEBRASKA: Atkinson, Holt Co., *Bates* (NY). NEW HAMPSHIRE: Brookline, Hillsboro Co., *Wright* (WIS); Concord, *Sargent* (NY). NEW JERSEY: Fort Lee, Bergen Co., *Enequist* 504 (NY); Wildwood, Cape May Co., *Pollard* (US); Farmingdale, Monmouth Co., *Taylor* 1783 (NY); Plainfield, *Tweedy* (US, NY); Hartford, Burlington Co., *Redfield* 555 (MO). NEW YORK: Piseco Lake, Hamilton Co., *Muenscher & Lindsey* 3439 (MO, G); Sevey, St. Lawrence Co., *House* 20708 (NY); Colton, *Phelps* 1600 (NY, G). NORTH CAROLINA: Middlesex, Nash Co., *Godfrey & White* 7008 (MO). OHIO: Oxford, Erie Co., *Moseley* (US, G); Portsmouth, Scioto Co., *Lapham* (WIS). OREGON: Cranberry bogs, Bandon, Coos Co., *Kranick* (OS). PENNSYLVANIA: Natrona, Allegheny Co., *Shafer* 9767 (GA, UP); Hopewell, Bedford Co., *Berkheimer* 3434 (UP); Berwick, Columbia Co., *Fosberg* 15225 (UP, G); Tinicum, Delaware Co., *Stone* 5156 (UP, NY, G); Mouth of Tucquan Creek, Lancaster Co., *Heller & Halbach* (NY, G); Peach Bottom, Lancaster Co., *Small* (NY, MO, US); Freeport Junction, *Koenig* (MO, WIS, US, G). RHODE ISLAND: Providence, *Collins* (MO). SOUTH CAROLINA: Socastee, Horry Co., *Doubles* (NY). TENNESSEE: McDonald's Place, Fentress Co., *Sharp & Shanks* 1552 (TENN); Bird Creek, Sevier Co., *Smith & Jennison* 3704 (TENN). VIRGINIA: Elko, Henrico Co., *Wherry & Pennell* 12522 (MO); Townsend, Northampton Co., *Fernald, Long & Fogg* 5383 (NY, G); Wakefield, Sussex Co., *Fernald & Long* 14953 (US, G). WEST VIRGINIA: Falling Run, Monongalia Co., *Millspaugh* 97 (NY); Upshur Co., *Pollock* (MO). WISCONSIN: Turtle Lake, Barron Co., *McLaughlin* 1899 (WIS); Barnes, Bayfield Co., *Fassett* 7148 (WIS); Arena, Iowa Co., *Levi & Rose* (WIS). NOVA SCOTIA: Cape Breton, *Rousseau* 35633 (NY); Upper Wood's Harbor, Shelburne Co., *Fernald & Fassett* 24179 (NY, G); Sable Is., *St. John* 1277 (NY, G). ONTARIO: Brule Lake, Algonquin Park, *Macoun* 22386 (NY, MO); Temagami Forest Reserve, *Watson* 6889 (WIS, G). QUEBEC: Calumet, Argenteuil Co., *Marie-Victorin & Rolland-Germain* 55115 (MO); Hull, *Ouimet & Fassett* 18126 (WIS).

The northeastern form of *V. lanceolata* (subsp. *lanceolata*) has been "well defined and properly understood" (Brainerd, 1905). Recently Fernald (1950) accepted Weatherby and Griscom's classification (1934) of the southeastern form (*V. vittata* of some authors) as a variety of the species. I have not examined the type of *V. lanceolata* L., which is deposited in the Linnaean Herbarium, but I have seen a photograph of it, on deposit in the Chicago Natural History Museum. The Linnaean type, of course, automatically becomes the type also of subsp. *lanceolata*.

V. lanceolata subsp. *lanceolata* is more or less uniform in appearance from eastern Canada and New England through Minnesota and Wisconsin and in the specimens found in cranberry marshes in Oregon and Washington. Its most distinguishing feature is its leaf shape, which is truly lanceolate, the lamina being from 3 to 5 times as long as broad and broadest below the middle. Fernald (1949) pointed out a difference in vegetative productivity between *V. lanceolata* and *V. primulifolia* which I am unable to confirm from my studies.

1a. **Viola lanceolata** L. subsp. **vittata** (Greene) stat. nov.

V. vittata Greene. Pittonia 3:258. 1898. *V. denticulosa* Pollard. Bull. Torr. Bot. Club 28:475. 1901. *V. lanceolata* L. var. *vittata* (Greene) Weath. & Grisc. Rhodora 36:48. 1934.

This subspecies differs from subsp. *lanceolata* principally in leaf shape. The mature leaves of *V. lanceolata* subsp. *vittata* are almost linear, often 10 or more times as long as wide. They have very short petioles, especially when young. They vary from glabrous to rather heavily pubescent, especially so on the petioles and lower lamina surfaces. In addition the bractlets and sepals are narrower than those of *V. lanceolata* subsp. *lanceolata*.

V. lanceolata subsp. *vittata* grows from coastal Massachusetts south to Florida and west to eastern Texas. It is essentially a coastal plain species, but several collections from southern Indiana have been seen.

ALABAMA: Coastal plain, Mobile Co., *Graves* (MO). ARKANSAS: Malvern, Hot Springs Co., *Palmer* 29982 (MO.) DISTRICT OF COLUMBIA: Washington, *Ward & F.H.K.* (US). FLORIDA: Gainesville, Alachua Co., *Murrill* (MO); Indian River, Brevard Co., *Fredholm* 6239 (NY, G); Duval Co., *Fredholm* 5016 (NY, G); 11 mi. west of Avon Park, Hardee Co., *Deam* 64290 (DEAM); Highlands Hammock State Park, Highlands Co., *Deam* 64031 (DEAM); Fanlew, Jefferson Co., *Harper* (NY, G); Ft. Myers, Lee Co., *Standley* 103 (NY, G); Otter Creek, Levy Co., *Murrill* 616 (US, GA); 3 mi. east of Citra, Marion Co., *Murrill* 678 (US, MO); Osceola Co., *Fredholm* 6215 (NY, G); Polk Co., *Schallert* (NY, ND); Raiford, Union Co., *Murrill* (MO); DeLand, Volusia Co., *Harkness* (MO); Jacksonville, March, *Curtiss* 208 (NY, G, US, COTYPES). GEORGIA: 12 mi. nw. of Field Station, Baker Co., *Thorne & Muenscher* 2684 (GA); Statesboro, Bulloch Co., *Harper* 2166 (MO); 12 mi. west of Savannah, Chatham Co., *Cronquist* 4282 (MO, G, US); Near Brunswick, Glynn Co., *Cronquist* 4270 (GA); South of Wadley, Jefferson Co., *Harper* 2099 (MO, NY); Southeast of Valdosta, Lowndes Co., *Duncan* 1309 (GA); 5 mi. north of Camilla, Mitchell Co., *Eyles* 5936 (GA); Suwanee Lake, Ware Co., *Harper* 447 (NY). INDIANA: Hanover, Jefferson Co., *Young* 8464 (IND). LOUISIANA: Jennings, Jeff Davis Parish, *Palmer* 7623 (MO). MASSACHUSETTS: Sandwich, Barnstable Co., *Hoffman* (MO). MISSISSIPPI: Biloxi, *Brainerd* 178 (NY, G, MO); Ocean Springs, Jackson Co., *Skehan* (Mo, NY). NEW JERSEY: Egg Harbor, Atlantic Co., *Lettermen* (MO), Haddonfield, *Stone* 5158 (NY). NEW YORK: Long Pond, L. I., *Parker* 37 (NY). NORTH CAROLINA: Middlesex, Nash Co., *Godfrey & White* 7008 (NY, G). SOUTH CAROLINA: McClellanville, Charleston Co., *Godfrey & Tryon* 258 (NY, MO, G); Beaufort, Beaufort Co., *Churchill* (MO). TEXAS: Angelina Co., *Reverchon* 3830 (MO); Chambers Co., *Tharp* 198 (NY, MO, G); Houston, *Hall* 25 (MO, US, NY). VIRGINIA: Corinth, Southampton Co., *Fernald & Long* 14368 (US, G).

V. vittata Greene was based on specimens from Texas (collected by E. Hall) and Florida (collected by both Canby and Curtis). A specimen was seen, *A. H. Curtis* 208, Jacksonville, Florida, March, 1898, on deposit at the New York Botanical Garden, which was labeled "cotype." *V. denticulosa* Pollard was based on a collection, *Harper* 724, from Douglas, Coffee Co., Georgia, Sept. 26, 1900. This was not seen, but the description and also annotated plants indicate only a particularly vigorous colony of *V. lanceolata* subsp. *vittata*. A specimen from the same location, collected by *Hendricks*, April, 1901 (G), is clearly subsp. *vittata*.

1b. **Viola lanceolata** L. subsp. **occidentalis** (Gray) stat. nov.

V. primulifolia L. var. *occidentalis* Gray. Bot. Gaz. 11:255. 1886. *V. occidentalis* (Gray) Howell. Fl. NW. Amer. 1:69. 1897.

This subspecies differs from the two preceding subspecies in the following ways: plants more vigorous, with thick, well-developed stolons; leaves wider, from 2-2.5 times as long as broad; and petals larger, the lower pair usually heavily bearded.

This subspecies is found at only a few localities in extreme northwest California and southwest Oregon.

CALIFORNIA: Gasquets, Del Norte Co., *Eastwood* 258 (MO). OREGON: Black Rock Lookout, Douglas Co., *Overlander* (OS); 4 mi. sw. of Cave Junction, Josephine Co., *Overlander* (OS); Near O'Brien, Josephine Co., *Thompson* 10285 (MO, NY); 6 mi. from Kerby, *Finch* 6062 (MO); Upland marshes near Waldo, June 5, 1884, *Howell* (WS, US, ISOTYPES); Waldo, *Howell* (NY, US, UC, MO).

The majority of taxonomists who have expressed opinions regarding this violet have considered it as most closely related to *V. primulifolia*, due to the very similar leaf shapes of the two violets. Mrs. Viola Brainerd Baird, however, recognized its closer resemblance to *V. lanceolata* (1942). In almost every character but leaf shape it more closely approaches *V. lanceolata*.

2. VIOLA PRIMULIFOLIA L. subsp. PRIMULIFOLIA

V. primulifolia L. Sp. Pl. 934, 1753, in part. *V. primulifolia* var. *acuta* Torr. & Gray, Fl. N. Am. 1:139. 1838. *V. acuta* Bigel, Fl. Bost., ed. II, p. 95. 1824.

Acaulescent from long, slender, prostrate or sometimes ascending rhizomes; vegetative reproduction by leafy stolons produced after petaliferous flowering as lateral branches which arise from near the terminal end of the rhizomes and immediately curve downward, ultimately lying horizontally just beneath the duff or on the surface of the ground; plants small, about 5 cm high in the spring, becoming 7-10 cm or more high in the summer and fall; rhizomes usually 2-4 mm in diameter near the summit, 1-1.5 mm in diameter farther back, occasionally thicker; peduncles, petioles, and leaf blades glabrous; leaf blades oblong to broadly ovate, the bases typically truncate or cuneate, obscurely crenate-serrate in the apical two-thirds, acute, thin; petioles winged; peduncles about as long as or shorter than the leaves, purple-specked at the curved upper end; petaliferous flowers with purplish-veined white petals, the spurred petal particularly so; sepals scarious-margined, light green, glabrous, ovate-lanceolate, auricled, the three main veins light green and conspicuous; lower pair of petals with a beard of only a few small hairs or occasionally glabrous; cleistogamous flowers sagittate, on erect peduncles shorter than the leaves; capsules light green, glabrous, ovoid; seeks black, 1-1.2 mm long.

V. primulifolia ranges from Nova Scotia, west to northern Indiana, and south to Florida and southern Texas. It is most frequent on the eastern coastal plain and piedmont. Two subspecies are recognized here, both of which, however, rarely occur in a "pure" form. The typical subspecies is found most often in northeastern United States, and the villous subspecies in Florida and along the Gulf coastal plain. Intermediates between the two subspecies are very abundant throughout much of the range. The hypothesis, to be discussed in a later paper, has been developed that subspecific distinctions have been partially obliterated by continued introgression.

CONNECTICUT: Southington, *Bissell* 32 (MO); Grove Beach, Middlesex Co., *Enequist* 386 (NY). DISTRICT OF COLUMBIA: Anacostia, *Blanchard* (MO); Good Hope Hill, *Reynolds* (MO, WIS, US, G). INDIANA: Dune Park, Porter Co., *Cowles* (MO). KENTUCKY: Oil Springs, Clark Co., *Wharton* 4645 (TENN). MAINE: Whitneyville, Washington Co., *Knowlton* (DEAM); Union, Knox Co., *Graves* (MO). MARYLAND: Patuxent, Anne Arundel Co., *House* 982 (NY, G); Lanham, Prince George Co., *Maxon* 5906 (US, G). MASSACHUSETTS: Brewster, Barnstable Co., *Fernald & Long* 17187 (NY); Ludlow, Hampden Co., *Seymour* 553 (MO, G); Nantucket I., *Bicknell* 6360 (NY). NEW HAMPSHIRE: Milford, *Wheeler* 1740 (US). NEW JERSEY: Milltown, Middlesex Co., *Mackenzie* 3064 (NY, US, MO); Watchung, Somerset Co., *Moldenke* 4530 (NY); Hartford, Burlington Co., *Redfield* 569 (MO). NEW YORK: New York City, *Bicknell* 6358 (NY). NORTH CAROLINA: Ducker Mt., Buncombe Co., *Biltmore* 1079 (US). OHIO: Liberty Twp., Jackson Co., *Pontious & Bartley* 17 (NY). PENNSYLVANIA: Birch Run, Adams Co., *Tanger* 3464 (UP); Manada Gap, Dauphin Co., *McCubbin* (UP); Ohio Pyle, Fayette Co., *Bright* 213 (DEAM); Black River Bog,

Lehigh Co., *Pretz* 1173 (NY); York Co., *Catfelter* (MO). RHODE ISLAND: Providence, *Collins* (US). TENNESSEE: Herbert Domain, Bledsoe Co., *Sharp* 1358 (TENN); McDonald's Place, Fentress Co., *Shanks* 1550 (TENN); Rockford, Roane Co., *Jennison & Anderson* (MO, G); Fall Creek Park, Van Buren Co., *Iltis* 3374 (TENN). VIRGINIA: Cowden, Alexandria Co., *Standley* 11370 (US); White Pine Lodge, Giles Co., *Iltis* 2164 (TENN); 3 mi. west of Williamsburg, James City Co., *Killip* 40152 (US). WEST VIRGINIA: Bucklin, Upshur Co., *Pollock* (US); Terra Alta, Preston Co., *Steele* 268a (NY). CAPE BRETON: Sydney, *Churchill* (MO). NOVA SCOTIA: Salmon Lake, Yarmouth Co., *Fernald, Long & Linder* 21926 (NY, MO, G).

The type of *V. primulifolia* L. is in the Linnaean Herbarium and was not available for this study. However, a photograph of it, on deposit in the Chicago Natural History Museum, has been seen. Two apparently authentic specimens of *V. acuta* collected by Bigelow from "Near Boston" are in the collection of the New York Botanical Garden, and these were examined in the course of this study. *V. primulifolia* is responsive phenotypically to various habitat extremes, and a number of forms and "species" have been segregated from it. These are mostly reduced to synonymy by Griscom (1936).

2a. **Viola primulifolia** L. subsp. **villosa** (A. Eaton) stat. nov.

V. primulifolia L. var. *villosa* A. Eaton, Manual, 5th ed., p. 443. 1829. *V. primulifolia* L. Sp. Pl. 934. 1753, in part.

This subspecies differs from subsp. *primulifolia* in having typically villous petioles and lower leaf blade surfaces; occasionally the upper lamina surfaces are also pubescent. In addition, this subspecies usually has slightly cordate leaf bases. The type of *V. primulifolia* L. var. *villosa* A. Eaton was not seen.

ALABAMA: Birmingham, Jefferson Co., *Palmer* 35330 (MO, G); Auburn, Lee Co., *Earle & Baker* 1662 (NY, G); Marshall Co., *Harbison* (US). ARKANSAS: High Point, Garland Co., *Palmer* 24538 (MO); Texarkana, Miller Co., *Trelease* (MO). FLORIDA: Gainesville, Alachua Co., *Murrill* (MO); Duval Co., *Fredholm* 5063 (US, NY, G); 7½ mi. sw. of Sebring, Highlands Co., *Deam* 64268 (DEAM); Hillsborough Co., *Fredholm* 6267 (NY, G); Eustis, Lake Co., *Nash* 339 (MO, NY, US, G); Marion Co., *Murrill* 662 (US); Orlando, Orange Co., *Palmer* 38335a (MO); St. Petersburg, Pinellas Co., *Deam* 4048 (DEAM); Lake Helen, Volusia Co., *Deam* 1652 (DEAM); Jacksonville, *Curtiss* 4517 (MO, US); Braidentown, *Tracy* 7527 (MO, NY, WIS, G). GEORGIA: McKaskey & Stamp Creeks junction, Bartow Co., *Duncan* 8189 (GA); Charlton Co., *Harper* 412 (NY); Near Moultrie, Colquitt Co., *Harper* 1675 (MO, NY, G); Lookout Mt., Dade Co., *Cronquist* 4825 (MO, GA, US); 19 mi. west of Savannah, Effingham Co., *Cronquist* 4384 (MO, US); North of Darien, McIntosh Co., *Cronquist* 4930 (GA, US); Tallulah Falls, Rabun Co., *Small* (MO, NY). LOUISIANA: 7 mi. south of Ruston, Lincoln Parish, *Anderson & Hubricht* (MO); Covington, St. Paul's, *Arséne* 11930 (NY); Seale, *Brainerd* (MO, NY); Natchitoches Co., *Palmer* 7229 (MO). MISSISSIPPI: 3 mi. so. of Hazelhurst, Copiah Co., *Ownbey* 1175 (MO); Biloxi, *Brainerd* (MO, G); Biloxi, *Tracy* 6548 (MO, NY, US); Saratoga, *Tracy* 8245 (NY, WIS, G). OKLAHOMA: Page, Leflore Co., *Blakeley* 1475 (NY, G). SOUTH CAROLINA: 2½ mi. ne. of Augusta, Aiken Co., *Radford* 30 (GA); Near Columbia, Richland Co., *Chapman* (GA). TEXAS: Texarkana, Bowie Co., *Palmer* 29653 (MO); Gonzales Co., *Tharp* (MO); Near Gauze, Milam Co., *Tharp* 43-456 (NY, MO, G); 3 mi. so. of Newton, Newton Co., *Cory* 52652 (US).

3. VIOLA MACLOSKEYI Lloyd subsp. MACLOSKEYI

V. macloskeyi Lloyd. Erythea 3:74. 1895. *V. anodonta* Greene. Pittonia 5:32. 1902. *V. blanda* Willd. var. *macloskeyi* (Lloyd) Jepson. Man. Fl. Pl. Cal., 648. 1925.

Acaulescent from long, slender, prostrate or somewhat ascending rootstocks producing long, slender, creeping, leafy stolons from near the apical end; plants small, generally 1

cm or less to 3 cm tall, occasionally 6-8 cm tall in late summer; leaf blades glabrous on both sides or heavily pubescent on the lower surface, heart-shaped, obtuse or acute, cordate at the base, usually shorter than the petioles; petioles green, with glabrous or sometimes ciliate wings, varying considerably in length, elongating after flowering; petaliferous flowers small; sepals light green, with a wide scarious margin, glabrous, linear-lanceolate to ovate-lanceolate; petals white, the three lower ones with dark purple veins, these sometimes coalescing enough to give the whole corolla a violet appearance; upper petals broadly obovate; lateral petals commonly with a heavy beard; cleistogamous flowers small, on erect or nodding peduncles produced in summer; capsules green, ellipsoid-cylindric; seed almost black when mature, about 1 mm long, rounded at base, ovoid.

Viola macloskeyi subsp. *macloskeyi* is found only in California, extreme western Nevada, and in Oregon, where it meets the much more widespread *V. macloskeyi* subsp. *pallens*, which occurs from northernmost Quebec and Labrador south to the Great Smoky Mountains in Tennessee and North Carolina and west to the northern and middle Rocky Mountains, the Pacific coast states, and British Columbia.

CALIFORNIA: Lake Alpine, Alpine Co., *Allen* 515 (UC); Colby, Butte Co., *Austin* 571 (MO, US); Jonesville, Butte Co., *Copeland* 661 (MINN, MO, NY, UC, G); Pine Ridge, Fresno Co., *Hall & Chandler* 133 (MO, MINN, UC); Bear Creek canon, Fresno Co., *Hall & Chandler* 568 (MINN, UC); Plaskett meadows, Glenn Co., *Ownbey & Ownbey* 1721 (MINN, WS, NY, G); Mt. Hull, Lake Co., *Hall* 9553 (UC); Willow Creek, Madera Co., *Constance* 2371 (UC, NY, G); Yosemite National Park, Mariposa Co. *Schreiber* 1732 (UC); Pine City, Mono Co., *Coville & Funston* 1831 (US); Yuba R. below Cisco, Placer Co., *Heller* 12689 (CLOKEY, OS, WIS, MO, NY, G); Bluff Lake, San Bernardino Co., *Parish* 3015 (US, MO); Mt. Shasta, Siskiyou Co., *Brown* 419 (MINN, US, NY); Farewell Gap, *Purpus* 5666 (MO, US, G). NEVADA: Marlett Lake, Washoe Co., *Baker* 1289 (MO, NY, US, UC, G). OREGON: Four Mile Lake, Klamath Co., *Applegate* 2513 (US); Crater Lake, *Gorman* 496 (US); Mt. Hood, July 22, 1894, Lloyd, ISOTYPE of *V. macloskeyi* (NY).

Lloyd designated no specific type for *V. macloskeyi*, but based it upon specimens he had collected the "previous summer" (1894) at Mt. Hood, Oregon. A specimen was seen that Lloyd collected on Mt. Hood in 1894 (*F. E. Lloyd, s. n.*, Mt. Hood, Oregon, July 22, 1894) which is on deposit in the herbarium of the New York Botanical Garden. The type of *V. anodonta* Greene was not seen, but the species description and the point of origin of the type collection (*Mrs. Peckinpah, s. n.*, Fresno Co., California) mark it as typical *V. macloskeyi* subsp. *macloskeyi*.

3a. VIOLA MACLOSKEYI Lloyd subsp. PALLENS (Banks) M. S. Baker, Madrono 10:110-128. 1949.

V. rotundifolia β *pallens* Banks ex D.C. Prodr. 1:295. 1824. *V. pallens* (Banks) Brainerd. Rhodora 7:247. 1905.

This subspecies differs from *V. macloskeyi* subsp. *macloskeyi* in having laminas with larger and less widely spreading basal lobes, better developed stolons, and in usually having few or no hairs on the lower pair of petals. In addition, the number of teeth on one side of the lamina is much greater (10-15, as compared to 0-4 in *V. macloskeyi* subsp. *macloskeyi*), and the laminas are always glabrous on both surfaces.

CALIFORNIA: Spirit Lake, Siskiyou Co., *Howell* 15065 (CLOKEY). COLORADO: Chicken Creek, southern Colorado, *Baker, Earle & Tracy* 153 (MO); CONNECTICUT: Feirfield, *Eames* (US, G). DELAWARE: 2 mi. so. of Milton, Sussex Co., *Walker* 3323

(US). INDIANA: Washington Twp., Blackford Co., *Deam* 705, 1108 (NY, DEAM, WIS); 5 mi. east of Lagrange, Lagrange Co., *Deam* 33778 (DEAM); Mineral Springs, Porter Co., *Nieuwland* 11665 (MO); Jackson Twp., Wells Co., *Deam* 977 (MO, NY, DEAM); Clarke, *Umbach* (MO, WIS, NY, G). MAINE: Fort Kent, Aroostook Co., *Churchill* (MO); Foxcroft, Piscataquis Co., *Fernald* 229 (MO, WIS, US, NY, G); Ocean Park, York Co., *Moldenke* 1575 (NY). MARYLAND: Pataspco Forest, Howard Co., *Plitt* 333 (US). MASSACHUSETTS: Ludlow, Hampden Co., *Seymour* 552 (MO, NY, G); West Roxbury, *Forbes* (MO, G). MICHIGAN: Vicksburg, Kalamazoo Co., *Rapp* 4495 (NY); Sault St. Marie, Sugar Is., *Churchill* (MO, G); Isle Royale, *Stuntz & Allen* 859 (WIS). MINNESOTA: Holyoke, Carlton Co., *Lakela* 4739 (MO, NY, MINN); Itasca Park, Clearwater Co., *Grant* 3233 (NY, MO, MINN); Longworth, Roseau Co., *Moore & Moore* 11388 (WIS); Duluth, St. Louis Co., *Lakela* 1945 (WIS, MINN); Two Harbors, *Sheldon* (US, WIS). MISSOURI: 5 mi. ne. of Pickle, St. Genevieve Co., *Steyermark* 464 (MO). MONTANA: Lake Waukena, Beaverhead Co., *Hitchcock & Muhlick* 13155 (WS). NEVADA: Copper Basin, Elko Co., *Maguire & Holmgren* 22379 (UC). NEW HAMPSHIRE: Spofford, Cheshire Co., *Moldenke* 9482 (NY); Mt. Washington, Coos Co., *Fassett* 16054 (WIS). NEW JERSEY: Clifton, Passaic Co., *Nash* (US); Budd's Lake, *Mackenzie* 8203 (NY). NEW YORK: Conquest, Cayuga Co., *Wiegand* 6831 (MO, G); Turedy Lake, Columbia Co., *Beals* (NY); Mt. Marcy, Essex Co., *Fassett* 10723 (WIS); Black Rock Forest, Orange Co., *Raup* 7501 (NY, G); Sneeders Landing, Rockland Co., *Taylor* 111 (NY); McLean bog, Westchester Co., *Bicknell* 6105 (NY); Thousand Is., *Bicknell* (NY). NORTH CAROLINA: Newland Bog, Avery Co., *Cain & Duncan* 202-2 (TENN); Blowing Rock Mt., Watauga Co., *Small & Heller* 483 (MO). OHIO: Berea, *Ashcroft* (MO); Cleveland, *Ashcroft* (US, MO, G). OREGON: 6 mi. west of Mackenzie Pass, Deschutes Co., *Hitchcosk & Martin* 4849 (US); Black Rock Lookout, Douglas Co., *Overlander* (OS); Near MacKenzie Pass, Lane Co., *Gilkey* (OS). PENNSYLVANIA: Tarentum, Allegheny Co., *Koenig* (US); Slippery Rock, Butler Co., *Russell* 267 (UP), Roaring Run, Centre Co., *Mathias* 1089 (NY); Girard, Clearfield Co., *Weiserfield* 197 (UP); 5 mi. sw. of Linesville, Crawford Co., *Graham* 430 (ND); Shorty's Place, Fulton Co., *Wagner* 9186 (UP); Collins, Lancaster Co., *Brubaker* 253 (UP); Buck Hill Falls, Monroe Co., *Stone* 5483 (UP); Penn's Creek P.O., Snyder Co., *Wade* 923 (UP); Muncy Valley, Sullivan Co., *Fosberg* 15030 (UP). RHODE ISLAND: Providence, *Collins* (US, G). TENNESSEE: Cades Cove, Blount Co., *Jennison* 2562 (TENN); Roan Mt., Carter Co., *Cain & Duncan* 214 (IND). UTAH: Uinta Basin, *Graham* 8176 (MO). VERMONT: Middlebury, *Brainerd* (MO, G); Mt. Mansfield, *Greenman* 1371 (MO). VIRGINIA: Mountain Lake, *Brown* (NY). WASHINGTON: Horseshoe Lake, Kitsap Co., *Warren* (WS); Seattle, *Bardell* (MO). WEST VIRGINIA: Canaan Mt., Tucker Co., *Davis & Davis* 5519 (TENN, G). WISCONSIN: St. Croix R., Burnett Co., *Wilson* 173 (WIS); Madison, Dane Co., *Chase* (WIS); Brule R., Douglas Co., *Thomsen* 5398 (WIS); Lake Mills, Jefferson Co., *Fassett* 7125 (WIS); Clifton, Monroe Co., *Roden* (WIS); Appleton, Ontagamie Co., *Smith* 219 (WIS); Brookfield, Waukesha Co., *Dickinson* (WIS). WYOMING: U. of Wyom. summer camp, Albany Co., *Greenman & Greenman* 6159 (MO); Shoshone National Forest, Park Co., *Williams & Williams* 3635 (MO, G). BRITISH COLUMBIA: Beaver Lake, Kootenay, *Anderson* 516 (WS); Illecillewaet Valley, Glacier, *Brown* 274 (MO, G). CAPE BRETON: Grand Lake, Sydney, *Churchill* (MO). LABRADOR: Caribou I., *Macfarlane* (US). NEW BRUNSWICK: Bay du Vin, Miramichi, *Fowler* (US). NEWFOUNDLAND: Grand Falls, *Fernald & Wiegand* 5881 (NY, G); Bay of Islands, *Waghorne* (NY, G); St. Pierre, (NY, G). NOVA SCOTIA: Arichat, Richmond Co., *Rousseau* 35594 (NY); Sable Is., *St. John* 1279 (NY). ONTARIO: Big Is., Georgian Bay Is., *McDonald* 518 (US, WIS); Algonquin Park, *Macoun* (NY). PRINCE EDWARD ISLAND: Mt. Stewart, Queens Co., *Fernald* 7785 (NY, G). QUEBEC: Georgeville, *Churchill* (MO, G); Lac Tremblant, Terrebonne Co., *Churchill* (MO, G); 88 mi. no. of Mont-Laurier, *Marie-Victorin* 410 (MO, G).

4. VIOLA RENIFOLIA A. Gray, Proc. Am. Acad. 8:288. 1870.

V. mistassinica Greene, Pittonia 4:5. 1899. *V. Brainerdii* Greene, Pittonia 5:89. 1902. *V. renifolia* Gray, var. *Brainerdii* (Greene) Fernald, Rhodora 14:88. 1912.

Acaulescent from rather short, relatively thick, usually vertical but occasionally ascending rootstocks; no vegetative stolons produced, but occasionally short, "raceme-like" stolons

bearing cleistogenes are produced in the late summer; leaves short, blades longer than the petioles, at least in the spring, reniform in shape with shallow sinuses and blunt, rounded apices, either completely glabrous, heavily pubescent, or intermediate between these two extremes; hairs, when present, long and fine on the lamina and short on the lamina margin; petaliferous flowers with light green, scarious-margined, ovate-lanceolate sepals; petals white and beardless, very rarely with a few hairs; lower pair of petals short, reniform or obovate; cleistogamous flowers and capsules on deflexed peduncles, borne in a prostrate position until maturity of the capsules when the peduncles become erect or ascending; capsules ovoid, reddish-brown or purple-flecked, sometimes almost completely purple; seeds smooth, 1.6-2 mm long when mature.

V. renifolia has been collected from Newfoundland westward in the Great Lakes region to Minnesota and thence northwestward into Alberta and British Columbia, with disjunct stations in the Black Hills of South Dakota.

COLORADO: Minnehaha, *Clements & Clements* 242 (MO, G). CONNECTICUT: Cornwall, *Eames & Starr* 10962 (DEAM, G). MAINE: Fort Fairfield, Aroostook Co., *Fernald* 15 (NY, US, MO, G); Fort Kent, *Mackenzie* 3513 (NY, DEAM, MO). MASSACHUSETTS: Greenfield, Franklin Co., *Churchill* (MO). MICHIGAN: Round Lake, Emmet Co., *Fallass* (DEAM); Phoenix, Keweenaw Co., *Hermann* 7729 (MO); Alma, *Davis* (MO, NY, US). MINNESOTA: Aiken Co., *Sandberg* 836 (US, NY); Sea Gull Lake, Cook Co., *Lakela* 3686 (MO); Angle Inlet, Lake of the Woods Co., *Moore & Moore* 11132 (US); Two Harbors, Lake Co., *Sheldon* 4715 (WIS, ND, MINN, G). MONTANA: Madison R. near Yellowstone, *Rydberg & Bessey* 4536 (US, NY). NEW HAMPSHIRE: Hanover, Grafton Co., *Sherman* (MO); Randolph, *Maxwell* (NY). NEW YORK: Arkville, Delaware Co., *Mulford & Wilson* (NY); Bergen Swamp, Genesee Co., *Metcalf & Eames* 8484 (MO, G); Peterboro, Madison Co., *House* 22531 (NY); Jamesville, Onondaga Co., *House* 3600 (NY); Canton, *Phelps* 688 (NY, G). RHODE ISLAND: Lyndon, *M.E.C.* (NY). SOUTH DAKOTA: Custer State Park, Custer Co., *Palmer* 37386 (MO, G); Sylvan Lake, Black Hills, *Rydberg* 546 (US). VERMONT: Peacham, *Blanchard* (NY, MO); Salisbury, *Brainerd* (MO, NY, G); Monkton, *Pringle* (US, WIS, MO). WISCONSIN: 4 mi. so. of Delta, Bayfield Co., *Bergseng* (WIS); Whirlpool Rapids, Lincoln Co., *Cheney* 2034 (WIS); Glenbeulah, Sheboygan Co., *Fassett & Hoffman* 18147 (WIS). ALASKA: Near Tyoneck, *Woolsey* 4 (US). ALBERTA: Sulphur Mt., near Banff, *McCalla* 2406 (US, NY); Ft. Saskatchewan, *Turner* 63 (NY, G). BRITISH COLUMBIA: So. Fork of Moose R., *Riley* 79 (US). NEW BRUNSWICK: Northwest of St. Andrews, *Malte* 537.29 (US, G). NEWFOUNDLAND: Bay of Islands, *Howe & Lang* 1089 (NY, G). ONTARIO: Dunk's Bay, Tobermory, *Fernald* 7630 (NY, G); New Hamburg, *Umbach* (NY, US, MO, G); Edmonton, *White* (MO). PRINCE EDWARD ISLAND: O'Leary, Prince Co., *Fernald & St. John* 11130 (NY, G). QUEBEC: Waterloo, *Anselm* 313 (NY); Lac Tremblant, Terrebonne Co., *Churchill* (MO, G); Rivere du Loup, *Eggleston* 3063 (MO, NY, G); Montmorenci Falls, *Macoun* 66745 (NY, G).

Varietal or subspecific rank is not recognized in the present treatment for *V. renifolia* var. *Brainerdii*, due to the fact that no correlation was found between leaf pubescence and geographical distribution. *V. renifolia* var. *Brainerdii* was based upon a single leaf pubescence type. A detailed analysis of pubescence variation in the stemless white violets has appeared elsewhere (Russell, 1954a).

No type specimen was cited by Gray for *V. renifolia*. The types of *V. mistassinica* Greene and *V. Brainerdii* Greene (on which *V. renifolia* var. *Brainerdii* was based) were not seen, but the original descriptions place them with *V. renifolia* A. Gray.

5. VIOLA BLANDA Willdenow, Hort. Berol. 1:5. 24. 1806.

Acaulescent from long, slender, vertical, ascending, or sometimes prostrate rootstocks, producing long, slender, leafy stolons from near the apical end; plants 2-4 cm tall in the

spring, somewhat larger in summer and autumn; leaf blades about as long as broad, with narrow basal sinuses, becoming quite large in late summer, crenate with small, hard-tipped teeth as in most of the other stemless white violets; plants wholly glabrous except for sparse to rather thick pubescence of small, white hairs on the upper surfaces of the leaf lobes, sometimes spreading over the whole lamina surface; petioles and peduncles often spotted with red in their lower parts in nature, this, however, a character poorly shown on herbarium specimens; petaliferous flowers slightly fragrant; sepals light green with scarious margins, ovate-lanceolate in shape; petals white, the three lower ones purple-veined, lower pair of petals always completely glabrous, long, narrow, with acute apices, twisted; cleistogamous flowers and fruits on prostrate or sometimes ascending, short peduncles; capsules purple or purple-spotted, ovoid; mature seeds about 1.5 mm long, acute at the base, dark brown, and minutely rugose.

V. blanda occurs from New England to northern Georgia, with a single station known from Florida. It reaches the Atlantic coastal plain in the northeast and southern Indiana to the west. Reports of its occurrence outside these limits, particularly to the west (see Fernald, 1950), are apparently based upon misdetermined specimens of *V. incognita*, *V. macloskeyi* subsp. *pallens*, or *V. renifolia*. In the far west, *V. macloskeyi* subsp. *macloskeyi* has often been mistaken for *V. blanda*.

CONNECTICUT: Torrington, Litchfield Co., *Denslow* (NY). DELAWARE: Mt. Cuba, *Bicknell* (NY). FLORIDA: Winter Park, Orange Co., *Huger* (NY). GEORGIA: Tallulah Falls, Rabun Co., *Perry & Strahan* 949 (NY, G); Between Dahlonega & Blairsville, Union Co., *Cronquist* 5110 (US). INDIANA: 6 mi. nw. of Medora, Jackson Co., *Deam* 24777 (DEAM); 1½ mi. west of Belleview, Jefferson Co., *Deam* 24687 (DEAM). KENTUCKY: Pineville, Bell Co., *Mackenzie* 963 (NY); Mammoth Cave National Park, *Lix* 218 (US). MAINE: Ocean Park, York Co., *Moldenke* 1601 (NY). MARYLAND: Cockeysville, Baltimore, *Churchill* (MO, G). MASSACHUSETTS: Tyringham, Berkshire Co., *Vail* (NY); Mt. Toby, Leverett, *Churchill* (MO). NEW HAMPSHIRE: Peterborough, Hillboro Co., *Batchelder* (TENN). NEW JERSEY: Fort Lee, Bergen Co., *Enequist* 502 (NY); New Brunswick, *House* 17 (MO). NEW YORK: North Chatham, Columbia Co., *House* 21135 (NY); Oneida, Madison Co., *House* 1160 (NY); Ithaca, Tompkins Co., *Gershoy* 10386 (MO); Pattens Mills, *Burnham* (US, G). NORTH CAROLINA: Mt. Mitchell, Buncombe Co., *Pollard* (US, MO); Cataloochee Divide, Haywood Co., *Jennison* 3793 (TENN); Bucks Creek, McDowell Co., *Hyams* (MO); Bryson City, Swain Co., *Jennison* 4124 (TENN). OHIO: Mineral Springs, Adams Co., *Cain* (TENN); Cleveland, Cuyahoga Co., *Ashcroft* (WIS, MO, G); Columbia Twp., Meigs Co., *Jones* (NY). PENNSYLVANIA: Birdsboro, Berks Co., *Berkheimer* 87 (UP); Roaring Run, Centre Co., *Mathias* 1088 (NY); DuBois, Clearfield Co., *Wahl* 937 (UP, G); Caledonia, Elk Co., *Wahl* 620 (UP, G); Ohio Pyle, Fayette Co., *Jennings* 96 (ND, UP); Tucquan Creek, Lancaster Co., *Heller & Halbach* (NY, G); 5 mi. no. of Trout Run, Lycoming Co., *Wahl* 286 (UP, G); Martin's Creek, Northampton Co., *Bartram* (UP); Mintzers, Schuylkill Co., *Wagner* 923 (UP); White Deer, Union Co., *Wagner* 8136 (UP); Falls, Wyoming Co., *Glowenke* 66 (UP); York Furnace, York Co., *Stone* 2887 (UP). TENNESSEE: Stoney Creek Valley, Carter Co., *Sharp* 1435 (TENN); Shady Valley, Johnson Co., *Jennison, Sharp & Underwood* 852 (TENN); Polk Co., *Kearney* 94 (US); Monterey, Putman Co., *Cain & Sharp* 4347 (NY, TENN); Holston Mt., Sullivan Co., *Underwood & Sharp* 420 (TENN), VERMONT: Bristol, Brainerd (MO, G); Clarendon, *Kittredge* (NY). VIRGINIA: Konnarock, Washington Co., *Eggleston* 18607 (NY, G); Luray, Page Co., *Steele & Steele* 101 (MO, US, G). WEST VIRGINIA: Milton, Cabell Co., *Gilbert, Williams & Fletcher* 676 (MO, WIS, G); Beechwoods, Monongalia Co., *Millspaugh* 59 (NY); Near Buckher, Upshur Co., *Pollock* (MO).

A combination of any two of the following three characters serves to distinguish this species: lamina length/breadth ratio of about 1.00; lower pair of petals glabrous; pubescence on upper lamina surfaces only. Where this species comes in contact with *V. incognita*, there usually is morphological intergradation, due to relatively unrestricted intercrossing.

The type of *V. blanda* Willd. was not seen, but Willdenow's plate and original description indicate that its placement here is accurate.

6. VIOLA INCOGNITA Brainerd, Rhodora 7:248. 1905.

V. incognita Brainerd var. *Forbesii* Brainerd. Bull. Torr. Bot. Club 38:8. 1911.

Acaulescent from long, slender, vertical, ascending or prostrate rootstocks, producing long, slender, leafy stolons; plants 2-4 cm tall in the spring, much larger in the summer and autumn; leaf blades broadly heart-shaped, with well-developed and spreading basal lobes, acute at the apex, usually longer than the petioles when the plant is in petaliferous flower and somewhat shorter later in the growing season; leaf blades either pubescent on the upper surface only, pubescent on both surfaces, or pubescent on the lower surface only; pubescence, when on the upper surface of the lamina only, principally confined to the basal lobes; petioles and peduncles glabrous or pubescent; petioles narrowly winged; petaliferous flowers with light green, scarious-margined, ovate-lanceolate, glabrous sepals; petals white, purple-veined; lower pair of petals with a small, dense beard of short, white, clavate hairs, rarely glabrous, slightly obovate, blunt, and straight; cleistogamous flowers on prostrate or nearly prostrate peduncles, producing purple or purple-flecked capsules which are short-ovoid; mature seeds 1.6-2.0 mm long, narrowly elliptic, obtuse at the base, smooth, light brown in color.

V. incognita ranges from Newfoundland and southern Labrador, south to the mountains of eastern Tennessee and western North Carolina, and westward in the Great Lakes region to Minnesota. Where it occurs, it is usually the most abundant of the stemless white violets.

CONNECTICUT: Glastonbury, Hartford Co., *Denslow* (NY); Danbury, *Barnhart* 97, 105 (NY). INDIANA: 13 mi. nw. of Ft. Wayne, Allen Co., *Deam* 23736 (DEAM); Michigan City, La Porte Co., *Deam* 38499 (DEAM); Mineral Springs, Porter Co., *Nieuwland* 11666 (MO, NY); Jackson Twp., Wells Co., *Deam* (DEAM). KENTUCKY: Mammoth Cave National Park, *Lix* 414 (US). MAINE: Ft. Kent, Aroostook Co., *Churchill* (MO); Monhegan I., Lincoln Co., *Churchill* (MO); Baring, Washington Co., *Knowlton* (DEAM); Ocean Park, York Co., *Moldenke* 1573 (NY). MARYLAND: Laurel, *Standley* 13240 (NY). MASSACHUSETTS: Mt. Toby, Franklin Co., *Moldenke & Moldenke* 9643 (NY); Salisbury, *Eaton* (MO, US, WIS, G); Amherst, *Jesup* (NY, G). MICHIGAN: Round Lake, Emmet Co., *Fallass* (DEAM); Jacobsville, Houghton Co., *Hermann* 7641 (NY); Bass Lake, Livingston Co., *Ehlers* 2786 (WIS); Isle Royale, *Stuntz & Allen* 701 (WIS). MINNESOTA: Cloquet, Carlton Co., *Lakela* 4302 (MO); Itasca Park, Clearwater Co., *Moyle* 288 (MO, NY, DEAM, G); Gunflint Lake, Cook Co., *Butters & Buell* 385 (NY, G); Washington Co., *Moore & Thatcher* 13778 (MO, G, MINN). NEW HAMPSHIRE: Center Harbor, Belknap Co., *Hartmann* 195 (NY); Crawford Notch, Coos Co., *Churchill* (MO); Derry, Rockingham Co., *Batchelder* (MO). NEW JERSEY: Oradell, Bergen Co., *Mackenzie* 1170 (NY); Madison, Morris Co., *Mackenzie* 646 (DEAM); Cranberry Lake, Sussex Co., *Mackenzie* 1130 (NY). NEW YORK: Conquest, Cayuga Co., *Wiegand* 6833 (MO, G); Stamford, Delaware Co., *Taylor* 312 (NY); Saugerties, Greene Co., *Taylor* 1940 (NY); Sylvan Beach, Oneida Co., *House* 1189 (NY, G); North Spencer, Tioga Co., *Eames & MacDaniels* 2877 (MO, G); Woodland, Ulster Co., *Britton* (NY); Black Pond, Westchester Co., *Bicknell* 6094 (NY). NORTH CAROLINA: Cosby, Cocke Co., *Raper & Jennison* 3257 (TENN); Roan Mt., *Redfield* 5532 (MO). OHIO: Cleveland, *Ashcroft* (NY, WIS); Burton, Geauga Co., *Webster* (MO). PENNSYLVANIA: New Hope, Bucks Co., *True* 21 (UP); Upper Darby, Delaware Co., *Smith* (UP); Chinchilla, Lackawanna Co., *Charnell* 30 (UP); Kane, McKean Co., *Churchill* (MO); Marysville, Perry Co., *McCubbin* (UP); Sherwood, Philadelphia Co., *Stone* 5159 (UP, NY, G); Meiserville, Snyder Co., *Wagner* 7953 (UP); York Furnace, York Co., *Stone* 7797 (UP). RHODE ISLAND: Providence, *Collins* (US, G). TENNESSEE: Wolf Creek, Cocke Co., *Kearney* 613 (NY); Gregory's Bald, Sevier Co., *Cain & Duncan* 493 (TENN). VERMONT: Rutland, Rutland Co., *Eggleston* 1056 (MO, NY); Jamaica, Windham Co., *Moldenke & Moldenke* 9474 (MO, NY); Middlebury, *Brainerd* (MO, NY, G). VIRGINIA: Hull Gap, Iron Mts., Smyth Co., *Britton* (NY). WEST VIRGINIA: Milton, Cabell Co.,

Gilbert, Williams & Fletcher 676 (NY). WISCONSIN: The Dells, Adams Co., *Fassett* 9952 (WIS); Washington I., Door Co., *Fuller* 1489 (WIS); Mather, Juneau Co., *Hamerstrom* (WIS); Oconto, Oconto Co., *Almon* (WIS); Cedarburg bog, Ozaukee Co., *Cutler* 379 (WIS); Ontario, Vernon Co., *Fassett & Truman* 12977 (WIS); Hartford, Washington Co., *Quandt* (WIS). CAPE BRETON: St. Pierre, *Rousseau* 35598 (NY, G). NEW BRUNSWICK: Bass River, *Fowler* (WIS); St. Francis, *Knowlton* 23706 (WIS). NEWFOUNDLAND: Humber Arm, Bay of Is., *Fernald & Wiegand* 3702 (NY, G); Channel, *Howe & Lang* 908 (NY); Balena, *Palmer* 1317 (MO, NY, G). NOVA SCOTIA: Port Mouton, Queens Co., *Graves, Long & Linder* 21941 (NY, G); Mulgrave, Guysborough Co., *Rousseau* 35536 (NY, G). ONTARIO: Cache Lake, Algonquin Park, *Macoun* 21684 (MO, NY); Ottawa, *Rolland* 7220 (NY, G); Stokes Bay, Bruce Peninsula, *Krotkov* 9238 (WIS). PRINCE EDWARD ISLAND: Tignish, Prince Co., *Fernald, Long & St. John* 7794 (NY, G). QUEBEC: Mt. Albert, Gaspe, *Allen* (NY, G); Lake Park, Orford, *Chamberlain & Knowlton* (MO, G); Lac Tremblant, Terrebonne, *Churchill* (MO, G); Anticosti I., *Marie-Victorin* 4155 (NY, G); Les Trois Lacs, *Marie-Victorin* 18646 (NY, G).

This species derived its name from the fact that it passed unrecognized until 1905 when Brainerd separated it from *V. renifolia* and *V. blanda*, where it had been confounding specific descriptions for a long time. As with *V. renifolia*, the only named variety has not been recognized. *V. incognita* var. *Forbesii* was based upon a lamina pubescence form, which occurs sparingly throughout the range of the species. The type of *V. incognita* Brainerd (Moosalamoo Mt., Salisbury, Vt., May 5, 1903 & Aug. 14, 1905, *Brainerd*) is deposited in the Gray Herbarium. Brainerd designated no type for *V. incognita* var. *Forbesii*.

NATURAL HYBRIDS

The following natural hybrids involving the stemless white violets have either been described in the literature or have been observed by the present author. A separate paper (Russell, 1954b) has appeared analyzing several instances of hybridizatoin in nature, including numbers 1 and 8 below.

1. V. LANCEOLATA subsp. LANCEOLATA x V. MACLOSKEYI subsp. PALLENS

V. lanceolata x *V. pallens* House. N. Y. State Mus. Bull. 243-244:26. 1923. *V. modesta* House. Bull. N. Y. State Mus. 254:509. 1924.

2. V. LANCEOLATA subsp. LANCEOLATA x V. PRIMULIFOLIA subsp. PRIMULIFOLIA

V. lanceolata x *primulifolia* Dowell. Bull. Torr. Bot. Club 37:163-177. 1910.

3. V. LANCEOLATA subsp. VITTATA x V. PRIMULIFOLIA subsp. VILLOSA

Numerous specimens, apparently representing this hybrid, were seen in material examined from the southeastern states.

4. MACLOSKEYI subsp. PALLENS x V. PRIMULIFOLIA subsp. PRIMULIFOLIA

V. pallens x *primulifolia* Dowell. Bull. Torr. Bot. Club 37:163-179. 1910.

5. V. MACLOSKEYI subsp. PALLENS x V. MACLOSKEYI subsp. MACLOSKEYI

Specimens, probably representing this hybrid, were seen in material from Washington and Oregon.

6. V. BRITTONIANA x V. LANCEOLATA subsp. LANCEOLATA

V. Brittoniana x *lanceolata* Forbes. Rhodora 11:14-15. 1909.

Brainerd (1924) referred to this as the "most remarkable violet hybrid." It was found in the Charles River Meadows, Dedham, Massachusetts, in 1906, with both parents, and was completely sterile. This and the following hybrid are the only two known natural hybrids between members of the acaulescent white and acaulescent blue groups of the Section *Nominium* of *Viola*.

7. V. CUCULLATA x V. PRIMULIFOLIA subsp. PRIMULIFOLIA

V. cucullata x *V. primulifolia* Brainerd. Rhodora 11:115-116. 1909. *V. lavandulacea* Bicknell. Torreya 4:130. 1910.

This hybrid was found at Rosedale and Woodmere, Long Island, in 1903 and 1904, by Bicknell. It was completely sterile.

8. V. BLANDA x V. INCOGNITA

Hybridization between these two species is well known. Putative hybrids were seen by the author from several localities.

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Sugar Maple-Basswood Studies in the Forest-Prairie Transition of Central Missouri[1]

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Composition studies of sugar maple-basswood communities have been reported in Minnesota, (Daubenmire, 1936), Wisconsin, (Eggler, 1938), and in Iowa, (Aikman and Smelser, 1938). In Minnesota and Wisconsin the principal associate of the basswood, *Tilia americana* L., was the sugar maple, *Acer saccharum* Marsh. The black maple, *A. nigrum* Michx. f., in central Iowa replaced the sugar maple as a codominant species. In a later study in central Iowa red oak, *Quercus rubra* L., was reported as a common species in mesic sites, (Kucera, 1950). Red oak in Wisconsin was reported by Eggler as a third species of importance in the type. Red oak as well as American elm, *Ulmus americana* L., and slippery elm, *U. rubra* Muhl., were ranked next in importance in the Minnesota stands.

It is the purpose of this paper to present comparative data pertaining to hitherto-unreported maple-basswood examples in central Missouri. Steyermark (1940) reported sugar maple-white oak and sugar maple-bitternut associations in the Ozark region. These studies, however, generally excluded the forest-prairie transition in central Missouri. Settler reports (Ind. World Comm. Adv., 1880) referred to the timber resources of Boone County in which sugar maple and basswood as well as other species were considered abundant.

Location and Description of Study Area

In Boone County, in which the present study was conducted, a relatively flat subclimax prairie underlain by claypan occurs in the northeastern portions. Southward, the prairies merge with the more dissected, forested uplands. The County is bordered on the south by the Missouri River. Here, the region is characterized by forested loessial hills underlain by limestones dated from Ordovician through Mississippian ages (Unklesby, 1952). No glacial soils occur here in the study area although Kansan till is present several miles to the north. Fig. 1 shows the general relationship of forest and prairie soils in Boone County.

The river hill topography in which the study area was located is characterized by steep gradients, and deep, narrow ravines and valleys. Within this area of the generally common oak forest, in ravines and on protected slopes, remnant stands occur in which hard maple and basswood are leading dominants. While the region generally has been cut-over, two stands in isolated situations were considered representative of the original forest. One, however, was somewhat limited in areal extent (only 10 plots were studied), and is used for comparison only with the other larger area in which 40 plots were observed. Both stands, however, were characterized by a succession of size

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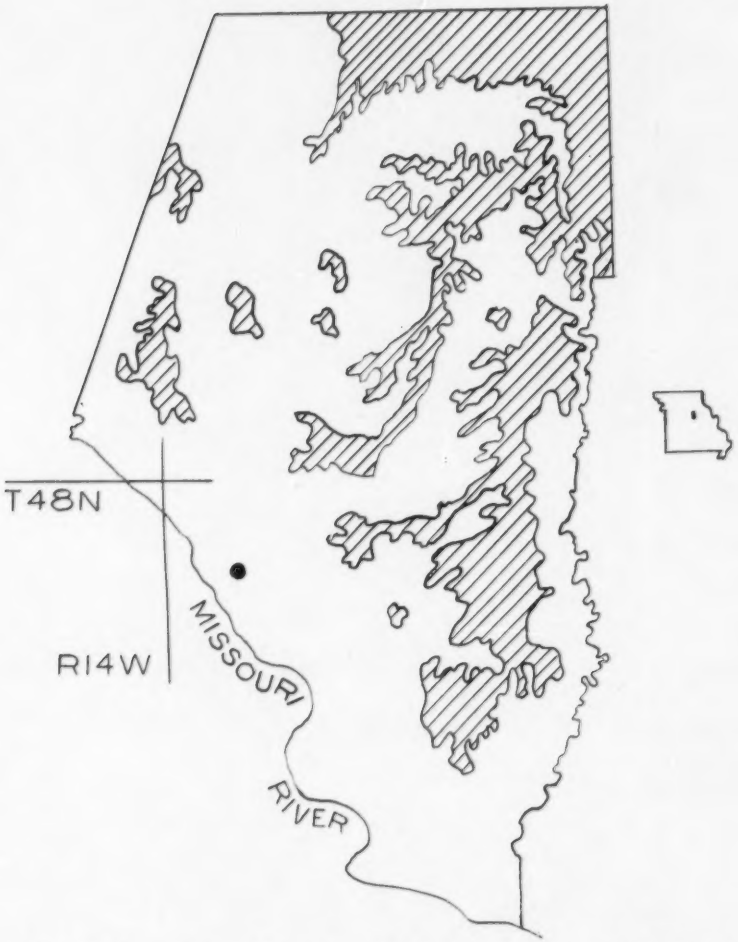

Fig. 1.—Boone County, Missouri, showing distribution of forest and prairie soils. Shaded areas represent the latter. Location of study area is designated by circle. The figure to the right indicates the position of Boone County in the State.

classes from seedlings to nearly 36 inches D.B.H. The major canopy of the dominant and codominant crown classes was well developed beginning at a height of from 50-55 feet. An average age of 165 years was determined for several white oak specimens between 27 and 30 inches D.B.H. The herbaceous flora was sparse, and a continuous and generally heavy forest litter was present.

In view of their restricted extent, it was thought justifiable to make a study of these woods before they too are altered by cutting and grazing. Admittedly, the study was limited by the fragmentary nature of the stands. Nevertheless, such data as were derived from these stands should be useful in better under-

standing the original composition and structure of mesophytic forest communities in central Missouri. Furthermore, this information serves as a basis of comparison with comparable forest development in several other widely scattered areas of the forest-prairie transition.

The larger of the two stand areas comprised about 15 acres of a northwest-facing slope located in section 17, T47N, R13W. The property holder is Tom Douglas of Columbia, Missouri. To his knowledge no removal of timber from the ravine had been effected. Surrounding woods showed evidence of past timber removal. The tract is not pastured presently, and judging from the type of ground flora and forest litter conditions, has not been in recent years.

The second stand fragment, occurring on a north-facing slope, was also in section 7, approximately 1/4 mile southeast of the first tract. It is in absentee ownership, and isolated by the Douglas property. The owner is John Schnabel of St. Louis. The soil type on both sites is classified as a Menfro silt loam. It is a loessial soil, deep and porous, with a medium-textured subsoil (Scrivner and Frieze, 1951).

General Climate

Mean annual temperature for central Missouri (Columbia Weather station, Boone County) based on 50 years of records (U. S. Weather Bureau, 1953) was 54.9°F. The high, 77.9° occurred in July, the low 30.5°, in January. Precipitation averaged 38.8 in., June and January being high and low months with 4.9 and 1.9 in. respectively.

Procedure

A topographic map of the Douglas tract was made. Sampling lines were drawn on an azimuth across the contour from the upper slope to near the bottom of the ravine. These lines were 1 1/2 chains apart. The random pairs method (Cottam and Curtis, 1949) was employed, using a 1 chain interval between plot centers. This plan produced a total of 40 plots, leaving a considerable buffer edge adjacent to disturbed woods. Tree species 4 inches D.B.H. and over were recorded and measured with diameter tape. Distance between paired trees was determined by tape measurement for making density calculations. Saplings and small trees 1 to 3.9 inches in diameter were counted and measured, using a milacre plot size (1 x 4 meters). Shrubs and vines were noted for frequency determinations. These plots were located on a line between paired trees, adjacent to the tree in the forward sector. For seedlings and herbaceous plants, a 1/4 milacre plot was employed for recording species presence. Density was not determined. This sample area, (1 x 1 meter), utilized the quarter section of the sapling plot away from the first tree.

Quantitative Studies

Field data were processed to determine frequency, density, and basal area. These criteria provided a measure of the degree of species occurrence, population abundance, and dominance. In turn, stand totals for each criterion served as a basis for determining the component importance of each species in the stands. An exception is noted regarding frequency for randomly-paired trees. Since the plot size varied, resultant frequency values are not quadrat frequencies in the usual sense where sampling area is kept constant. These values are

designated as random pair frequencies (Frp) to distinguish from the fixed-area frequency (F).

Douglas Woods.—In table 1 frequency, density, and basal area are recorded for the larger of the two stands. In this area *Acer saccharum* was the most abundant species in all size classes exceeding one inch. The total density for these classes was approximately 6½ times that for *A. nigrum*. The greatest difference in density was in the size classes below 10 inches. In these diameters, the ratio was about 8 to 1. Over 10 inches however, the ratio was less than two *A. saccharum* to one *A. nigrum*. This relative increase of *A. nigrum* in the larger diameters is reflected in the proportionately greater basal area per tree. On the basis of combined densities, the *Acer* group was clearly predominant in this stand. Data from table 1 would also indicate that sugar maple was the most uniformly distributed species in all classes including seedlings.

Tilia americana, basswood, was the next most important forest tree. Large diameters were characteristic of the species. One specimen measured 35.3 inches in diameter at breast height. The trees characteristically occurred in clumps. While seedlings were observed, they were not nearly as commonly distributed as the maple. The low frequency value, 10 percent, is indicative of a lack of uniformity of occurrence. In comparison, maple seedlings of either species or both occurred in over 52 percent of the quadrats. A similar observation regarding the scarcity of basswood seedlings was made by Daubenmire (1936). Following *Tilia* the next most prominent species in terms of density and dominance was *Ulmus rubra*. This species was also conspicuous in Minnesota stands. The combined values (above 1 inch D.B.H.) for *Acer* spp., *Tilia*, and *Ulmus* constituted 61 percent of the total density and 80 percent of the total basal area. *Quercus rubra*, red oak, though present was not of major importance in this stand. *Acer* spp. and *Tilia* were clearly indicated as leading dominants. The stand as a maple-basswood example, however, appeared not as distinctive as those in Wisconsin and Minnesota, when percentage densities and basal areas were compared. The decreasing frequency and abundance of these species, particularly sugar maple, south and westward in the prairie peninsula region has been noted by several authors. These trends to some extent may be indicated here.

Schnabel Woods.—As in the first site, the combined densities and basal areas attested to the general preeminence of the two species of maple in the second study area. In point of numbers, *Quercus rubra* was here an important overstory tree, exceeding basswood. These comparisons are shown in table 2. Basal areas were not significantly different between red oak and basswood. Specimens of the latter were again typically large. The combined totals for these four species comprised 61 percent of the stand density and 91 percent of the basal area. In comparing the two stands it is seen that *Ulmus rubra* ranked high in one and not in the other, while the converse was true for red oak. Another difference was the greater number of species in the first stand. Otherwise, the two areas were similar in the common predominance of *Acer* spp. and *Tilia*.

Importance Values.—In table 3 are presented summations of the relative values of frequency, density, and basal area for each species. This summation

TABLE 1.—Frequency, density, and basal area (sq. ft. D.B.H.) on an acre basis for tree species[2] in Douglas Woods.

Species	Individuals less than 1 in. D.B.H.	Individuals 1-3.9 in. D.B.H.			Individuals 4-10 in. D.B.H.			Individuals 10 in. D.B.H. and over.			Total	
	F-%	F-%	D	BA	Frp[3]-%	D	BA	Frp-%	D	BA	D	BA
Acer saccharum	40	20	200	3.86	35	52	8.70	13	19	32.81	271	45.36
A. nigrum	20	3	25	0.15	5	6	0.41	5	11	17.41	42	19.97
Tilia americana	10	10	175	3.08	13	20	5.20	10	13	60.20	208	68.48
Ulmus rubra[4]—U. americana	20	3	25	0.15	28	42	15.10	5	7	4.71	74	19.96
		3	25	0.15	3	3	0.91	....	....	....	28	1.05
Fraxinus americana	15	3	25	1.23	15	22	6.48	3	3	5.52	50	13.23
Quercus rubra	15	....	....	....	3	4	1.11	3	3	5.90	7	7.01
Gymnocladus dioica	5	3	25	0.85	....	....	....	3	3	4.10	28	4.95
Quercus muhlenbergia	3	3	25	1.23	10	13	3.40	....	....	....	38	4.63
Ostrya virginiana	5	10	75	2.40	....	....	....	....	....	....	75	2.40
Quercus alba	8	....	....	....	3	3	1.21	....	....	....	3	1.21
Fraxinus penn. var. subintegerrima	....	....	....	....	5	7	1.10	....	....	....	7	1.10
Celtis occidentalis	3	....	....	....	5	7	0.89	....	....	....	7	0.90
Carya cordiformes	....	5	50	0.31	3	3	0.40	....	....	....	53	0.71
Sassafras albidum	....	....	....	....	3	3	0.71	....	....	....	3	0.71
Cornus florida	15	....	....	....	5	7	0.50	....	....	....	7	0.50
Carya ovata	....	....	....	....	3	3	0.50	....	....	....	3	0.50
Asimina triloba	25	5	50	0.31	....	....	....	....	....	....	50	0.31
Staphylea trifolia	....	3	25	0.15	....	....	....	....	....	....	25	0.15
Prunus serotina	3	....	....	....	....	....	....	....	....	....	....	....
Fraxinus quadrangulata	5	....	....	....	....	....	....	....	....	....	....	....
Platanus occidentalis[5]	....	....	....	....	....	....	....	....	....	....	....	....
Total			725	13.87		195	46.62		59	130.64	979	191.13

[2] All species in this and other tables based on the nomenclature of Gray's Manual of Botany, Ed. 8, 1950.
[3] Random pair frequency
[4] Seedlings of *Ulmus* not differentiated in seedling stage
[5] Seedling observed outside sample plots

TABLE 2.—Frequency, density, and basal area (sq. ft. D.B.H.) on an acre basis for tree species in Schnabel Woods.

Species	Individuals less than 1 in. D.B.H.	Individuals 1-3.9 in D.B.H.			Individuals 4-10 in D.B.H.			Individuals 10 in. D.B.H. and over.			Total	
	F-%	F-%	D	BA	Frp-%	D	BA	Frp-%	D	BA	D	BA
Acer saccharum	30	30	300	3.40	10	8	2.69	30	24	51.01	332	57.10
A. nigrum	....	....	....	....	....	....	....	20	16	34.60	16	34.60
Tilia americana	....	....	....	....	....	....	....	20	20	64.50	20	64.50
Quercus rubra	10	....	....	....	....	....	....	30	26	58.56	26	58.56
Ulmus americana	....	....	....	....	....	....	....	10	8	8.92	8	8.92
Ostrya virginiana	10	20	200	2.80	10	8	0.70	....	....	....	208	3.50
Carya cordiformes	....	....	....	....	10	8	2.45	....	....	....	8	2.45
Quercus muhlenbergia	....	....	....	....	10	8	2.11	....	....	....	8	2.11
Cornus florida	....	....	....	....	10	8	2.00	....	....	....	8	2.00
Fraxinus penn. var. subintegerrima	20	....	....	....	10	8	0.70	....	....	....	8	0.70
Asimina triloba	20	....	....	....	....	....	....	....	....	....	....	....
Fraxinus quadrangulata	10	....	....	....	....	....	....	....	....	....	....	....
Cercis canadensis	10	....	....	....	....	....	....	....	....	....	....	....
Total			500	6.20		48	10.65		94	217.59	642	234.44

index for each species in the stand is the importance value (Curtis and McIntosh, 1951). The presentation of these data is for comparison with similar stands of the more northern forest-prairie transition. The total value comprising all species in the stand is 300. The relative importance of any species is indicated by the component part it contributes to the stand total. Thus, in the two stands studied, summation values would seem to emphasize the role of *Acer* spp. and *Tilia* as leading dominants common to both areas. The application of tentative climax adaptation numbers, some of which differ from those given by Curtis and McIntosh, indicated a continuum index for these stands between 2531 and 2542.

Lesser Vegetation.—The most prominent tree of the understory in both stands was *Ostrya virginiana* (Mill.) K. Koch (tables 1 and 2). Other species of less prominence included *Asimina triloba* (L.) Dunal and *Cornus florida* L. The latter is found in the upland forest throughout the Ozark region. It occurred only infrequently in the present stands. *Asimina triloba* was more common in the study areas, and typically is found in moist situations and stream bottoms. While *Ostrya* is common to both the Wisconsin and Minnesota stands, *Asimina* and *Cornus florida* apparently are not. These two species have more southern and eastern distributions. Other species reported in the present study, whose native ranges apparently are south and east of the forest areas being compared are *Sassafras albidum* (Nutt.) Neese and *Fraxinus quadrangulata* Michx. Both however occur in the southeastern part of Wisconsin.

In table 4 is a list of the remaining plants observed in the Douglas stand. No table is presented for the second study area although, generally, close agreement was indicated. Low frequencies were characteristic of the shrub and vine flora, *Celastrus scandens* L. appearing most often. A survey of the stand was made to find additional species not occurring in the plots. These are also shown. If densities had been recorded, *Symphoricarpos orbiculatus* Moench. would probably have had a relatively high value in comparison to its low frequency. The species occurred in dense though small clumps where light penetration was increased due to small canopy gaps.

TABLE 3.—Importance values for tree species in Douglas Woods and Schnabel Woods.

Species	Douglas Woods	Schnabel Woods
Acer spp.	102	106
Tilia americana	61	55
Ulmus rubra	46	....
Quercus rubra	10	57
Fraxinus americana	24	....
Ulmus americana	4	17
Quercus muhlenbergia	10	13
Fraxinus penn. var. subintegerrima	7	13
Cornus florida	7	13
Carya cordiformes	4	13
Ostrya virginiana	....	13
Gymnocladus dioica	6	....
Celtis occidentalis	6	....
Quercus alba	6	....
Carya ovata	4	....
Sassafras albidum	4	....
Total	300	300

TABLE 4.—Frequency values for plants found in ¼ milacre plots (1 milacre for shrubs and vines). 40 quadrats.

Species	Frequency—%	Species	Frequency—%
MOSSES		Galium Aparine	5
Mnium spp.	3	Asarum canadense	5
Eurynchium hians	3	Isopyrum biternatum	3
E. strigosum	3	Caulophyllum thalictroides	3
Thuidium delicatulum[6]	....	Desmodium glutinosum	3
FERNS		D. nudiflorum	3
Botrychium virginianum	3	Viola pensylvanica	3
Adiantum pedatum	3	Ruellia strepens	3
Polystichum acrostichoides[6]	....	Phryma Leptostachya	3
GRASSES AND SEDGES		Solidago ulmifolia	3
Brachyelytrum erectum	8	S. radula	3
Festuca obtusa	5	Corallorhiza Wisteriana[6]	....
Uniola latifolia	5	Dicentra Cucullaria[6]	....
Diarrhena americana[6]	....	Osmorhiza Claytoni[6]	....
Muhlenbergia sobolifera[6]	....	Erigenia bulbosa[6]	....
Carex albursina	33	SHRUBS AND VINES	
C. artitecta	8	Celastrus scandens	15
C. Jamesii[6]	....	Evonymous atropurpureus	8
OTHER HERBACEOUS PLANTS		Smilax tamnoides var. hispida	8
Eupatorium rugosum	28	Parthenocissus quinquefolia	8
Aster anomalus	18	Symphoricarpos orbiculatus	5
Geum canadensis	8	Vitis aestivalis	5
Sanicula marilandica	8	Corylus americana	3
Tovara virginiana	8	Menispermum canadense	3
Phlox divaricata	5	Rhus radicans	3
Blephilia hirsuta	5	Staphylea trifolia	3

[6] Plants not in plots but observed in stand area.

Among the grasses and sedges, the wide-leafed *Carex albursina* Sheldon was most common, followed by *C. artitecta* Mackenz. Grasses were infrequent. Two additional species were observed outside the plots. These were *Muhlenbergia sobolifera* (Muhl.) Trin. and *Diarrhena americana* Beauv. The most commonly-occurring wide-leafed herb was *Eupatorium rugosum* Houtt. It typically is found in moist, shaded sites, occurring throughout Missouri on circumneutral soils. Since the field work was performed in late summer, a number of vernal species may have been missed in the sample plots. However, several species were observed and recorded on earlier trips to the stand, for example *Corallorhiza Wisteriana* Conrad, and are presented here.

Soil Studies.—Soil-water, organic matter, and nutrient relationships are considered necessary chemical and physical aspects of study in correlating site characteristics and vegetation. No work in soil analysis was carried out in the present investigation. As further studies in forest composition are pursued in this transition region, such information concerning the edaphic environment will be included.

SUMMARY

Two forest stands in the forest-prairie region of central Missouri were analyzed. The stands, considered examples of undisturbed forest, were situated on north and northwest-facing slopes, underlain by deep, porous soils of loessial origin. The random pairs method cited previously was employed in

obtaining field data. Percentage frequency, density, and basal area were calculated for each species. The summation of these values was used to express species importance in the stand.

Calculations showed that the leading dominants common to both stands were collectively *Acer saccharum* and *A. nigrum*, and *Tilia americana*. *Ulmus rubra* and *Quercus rubra* were other prominent species, in one stand or the other. The most prominent species of the understory in both stands was *Ostrya virginiana*.

Tentative climax adaptation values were applied to data in determining a continuum index for each stand. The indices ranged from 2531 to 2542 out of a possible total of 3000. Additional stands are needed for further investigation.

Comparison of lesser vegetation with that of Wisconsin and Minnesota stands referred to previously indicated that certain species common to the Missouri forests drop out in northern portions of the prairie peninsula. These included *Asimina triloba*, *Cornus florida*, *Sassafras albidum*, and *Fraxinus quadrangulata*.

Studies of sugar maple-basswood stands in central Missouri on the southern edge of the prairie peninsula indicated similarity to those in more northern sections of the forest-prairie region.

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Moorefield Woods: Old-growth beech in Switzerland County, Indiana

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On October 15, 1952 a visit was made to Moorefield Woods, Switzerland County, in the southeast corner of Indiana. The purpose of the visit was to investigate reports of some very large beech trees (*Fagus grandifolia*) in the area. Now called the Community Park it was referred to as the "Celebration Woods" prior to its purchase by the Ebenezer Church in 1922. The returning veterans of the Civil War were honored here in 1865 and ever since a yearly celebration as well as family reunions have taken place. This type of use has caused the elimination of virtually all the reproduction but the remaining beech are beyond a doubt representative of the climax forest of this region. The area was surveyed in the space of only one day but the entire park was covered by quadrats and the results are complete and not merely a sample.

Physical Features

Geology.—The general area of the Moorefield Woods lies on the Dearborn upland at an altitude of 910 feet just north of the Ohio River and was formed from the old Lexington peneplain. Actually this area represents a highly dissected tableland with narrow ridges separated by long valleys. The original Lexington peneplain was probably raised during late Tertiary time to a general elevation of 900 to 1000 feet. The present upland is a result of differential erosion of upper Ordovician limestones and shales.

Glaciation.—The particular portion of the Illinoian glacier, which covered this area with till deposits, is known as the Louisville-Cincinnati lobe. In general, the deposit is rich in clay content but has less gravel today than subsequent, later, glacial deposits lying farther north.

Soils.—The soil types of the Moorefield Woods area consist of the Rossmoyne and Cincinnati silty clay loams. The soil profiles average from 10 to 12 feet deep and have been developed largely from Illinoian drift. The Rossmoyne has developed on the gently rolling upland portions of the area, while the Cincinnati is associated with the more sloping areas. Both soil types are members of the gray-brown podzolic family developed under a humid climate and hardwood forests. The Cincinnati type has good internal drainage; however, the Rossmoyne profile is somewhat sluggish, due to a clay accumulation at a depth of 20 to 30 inches. These soils are moderately acid through most of the profile. The pH reaction of these soils is 5.8 at the surface and ranges from 4.8 to 5.4 through the first 6 to 8 feet of the profile.

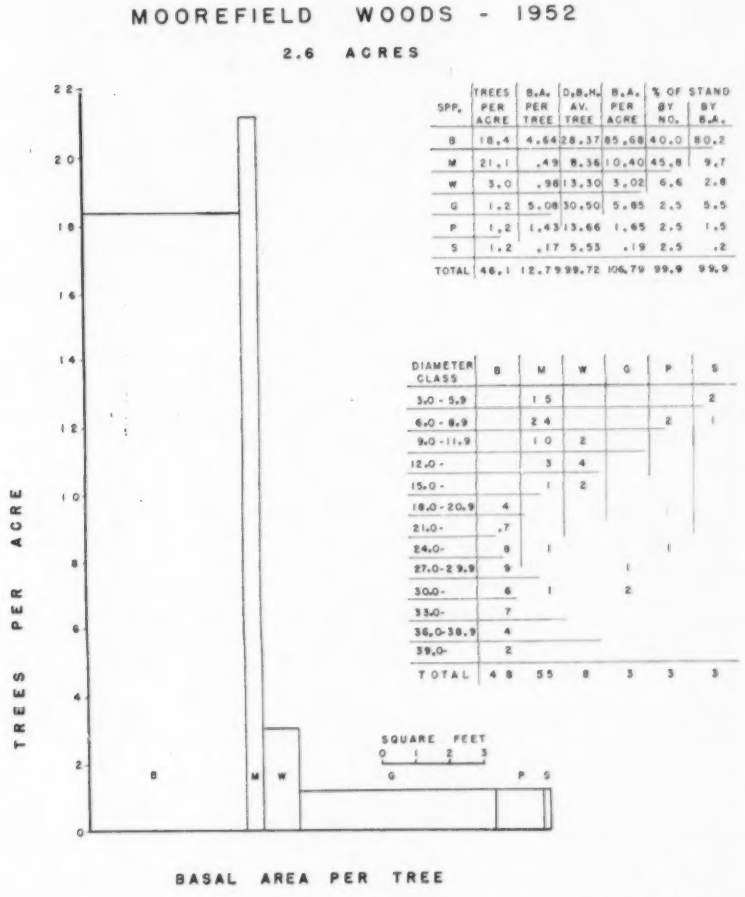
Climate.—The climate of Switzerland County, Indiana, is of the warm continental type, with considerable variation in temperature and precipitation. The mean temperatures of the three summer months average near 70° F, and the mean temperatures for the three winter months average near 35° F. The relative humidity averages about 70 percent for the entire growing season. The

[1] The author wishes to acknowledge Dr. A. A. Lindsey, J. E. Newman, Dr. G. L. Plummer, all of Purdue University, who assisted in the collection of the field data, and Dr. A. G. Vestal, of the University of Illinois, who rendered valuable criticism.

average annual precipitation is 41 inches, with about 25 inches of snowfall a year. The average frost-free season is 173 days, with the last frost in the spring occurring near April 25th, and the first autumn frost occurring about October 15th.

METHODS

The Woods was not so large but that the entire area could be quadratted. A series of transects were laid out by compass and measuring tapes, and every tree in the park was recorded as to position, species and basal area. Heights of certain of the taller trees were measured by means of an Abney level. Some



SPP.	TREES PER ACRE	B.A. PER TREE	D.B.H. AV. TREE	B.A. PER ACRE	% OF STAND BY NO.	% OF STAND BY B.A.
B	18.4	4.64	28.37	85.68	40.0	80.2
M	21.1	.49	8.36	10.40	45.8	9.7
W	3.0	.98	13.30	3.02	6.6	2.8
G	1.2	5.08	30.50	5.85	2.5	5.5
P	1.2	1.43	13.66	1.65	2.5	1.5
S	1.2	.17	5.53	.19	2.5	.2
TOTAL	46.1	12.79	99.72	106.79	99.9	99.9

DIAMETER CLASS	B	M	W	G	P	S
3.0 - 5.9		15				2
6.0 - 8.9		24			2	1
9.0 - 11.9		10	2			
12.0 -		3	4			
15.0 -		1	2			
18.0 - 20.9	4					
21.0 -	7					
24.0 -	8	1			1	
27.0 - 29.9	9			1		
30.0 -	6	1		2		
33.0 -	7					
36.0 - 38.9	4					
39.0 -	2					
TOTAL	48	55	8	3	3	3

Fig. 1.—Composition diagram, composition table and stand table for the area known as Moorefield Woods in Switzerland County, Indiana. (B, beech; M, sugar maple; W, black walnut; G, black gum; P, tulip poplar; S, silver maple.)

26 quadrats were surveyed and arranged into adjacent transects. Each quadrat was 100 links square making a total of 2.6 acres examined. Each tree was entered upon graph paper in its proper position along with abbreviated notes concerning the species and diameters. All heights measured were recorded. In

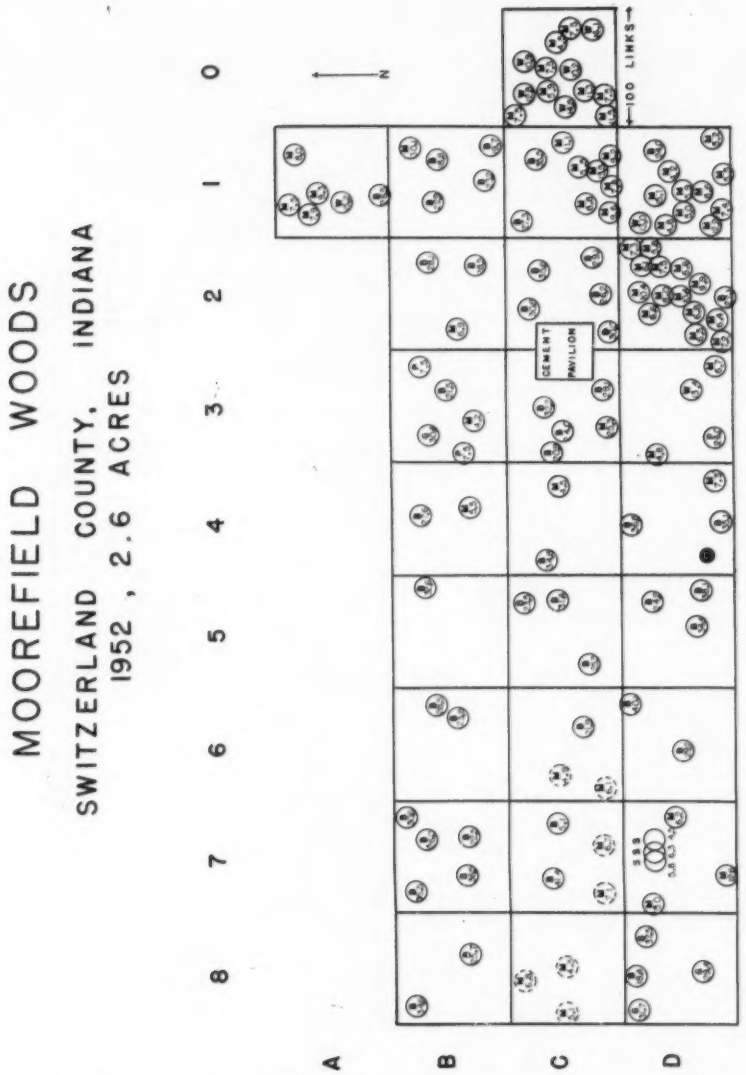


FIG. 2.—Diagrammatic map of Moorefield Woods showing positions, species and diameters of every tree. Interrupted circles represent planted trees which were not included in the calculated results. (Diameters to nearest tenth-inch.)

this way a permanent record has been made in the event that any future study is made of the area.

RESULTS

The data are probably most easily presented and interpreted by means of the accompanying composition diagram, composition table and stand table (fig. 1). It might be pointed out that the areas of the respective bars in the composition diagram reflect the relative basal areas per acre of each species which, as "cover," is probably one of the most important ecological measurements.

The map (fig. 2) is presented in order that future work on the area might be correlated more easily. Interrupted circles on this map record the positions of young sugar maples which have obviously been planted. These have been excluded from the data in the tables and diagram.

In addition to the other data the taller trees in the woods were measured for height. The tallest beech was 118 feet in height with a diameter of 35.1 inches. A tulip poplar of 26.0 inches diameter reached 95 feet in height.

Outside the transects were many other beech trees of very large dimensions. To the east of the park area were a number ranging from 35.4 to 39.4 inches in diameter. Near the entrance to the recreation area two very large beeches are noticeable and one of these with a diameter of 46.6 D.B.H. is believed to be the largest in the area.

DISCUSSION

The area in and about Moorefield Woods appears to be a very good example of the beech-maple association which is thought to be the climax in this part of Indiana. At the present time, however, the maple component has been eliminated due to differential lumbering. That the area once held sugar maple in quantity is beyond question since in a personal communication, Mrs Robert Hart of Vevay, Indiana, states that at one time her father worked the area as a sugar bush and made some quantity of syrup therefrom. Also the less disturbed area just to the east has quantities of sugar maple reproduction along with a few more or less mature trees although none have reached the extraordinary dimensions of the beech component. There is no reproduction of any kind within the park area but some maples have been planted in the western portion of the area and are evidently doing very well. True conclusions concerning the vegetation type can only be drawn from the accumulated data by considering the very large trees.

It is the author's belief that the beech tree near the entrance to the park (46.6 inches D.B.H.) establishes a new record for Indiana (Laughlin, 1947).

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Notes and Discussion

A New Record For Cladophora Balls*

In September 1953, on a field trip to Cayuta Lake, near Ithaca, New York, the author, in company with William E. Werner, Jr., discovered a supply of peculiar *velvet balls* at one point in the lake. Investigation proved them to be spherical balls of the alga, *Cladophora holsatica* Keutz., 1849, this identification later confirmed by Dr. G. W. Prescott of Michigan State University. The existence of this form of *Cladophora* has been known for some time, and Kindle (1934) says that Thoreau (in *Walden*, 1889?) refers to ". . . curious balls . . . composed apparently of fine grass or roots . . . perfectly spherical." These may well have been *Cladophora* balls, or *lake balls*, similar structures which are composed of grass particles, etc., and which are formed by the same methods.

Cladophora balls are formed by the mechanical action of waves, usually over a gently sloping sandy or gravelly bottom. The filaments of the alga are *rolled* by the water, and soon become entangled into a ball, or a mat-like mass which ultimately breaks up. These pieces then tend to become spherical, and the ball is formed. Collins (1909) says each ball is a densely branched individual, but the present writer feels the probability is greater that many *individual* filaments merely become intertwined. *C. holsatica* filaments show a tendency to branch repeatedly when the terminal cell is harmed (by the rolling wave action), and as a consequence of this branching, the compact, dense structure of the ball is formed (Acton, 1916). The shape of the ball is a purely mechanical function of the water habitat, as Brand (1902) has shown experimentally that this alga could exist in the form of ". . . Rasen, Polstern, und Ballen . . ." (turf, cushion, and balls).

* The writer wishes to thank Dr. W. C. Muenscher of Cornell University, and Dr. G. W. Prescott of Michigan State University, for their encouragement.

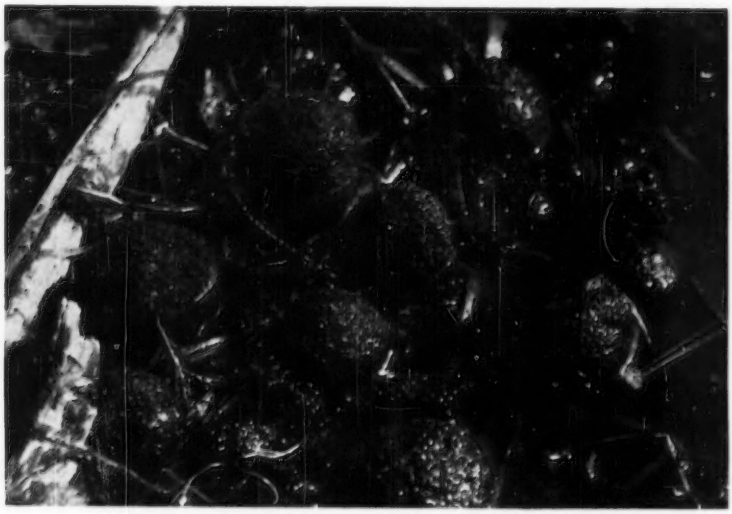

Fig. 1.—*Cladophora* balls at edge of water. Note also *Anacharis canadensis, Ceratophyllum demersum, Potamogeton epihydrus.* Cayuta Lake, Schuyler Co., N. Y. Sept. 1953.

Balls kept for nearly a year in the laboratory showed no change from the original spherical form, but this would be expected, since the filaments grow essentially equally in all directions, therefore would tend to preserve the ball form.

Reproduction in this particular form of *Cladophora* appears to have been little studied. Acton (1916) says that resting spores or hypnospores seem to have a reproductive function, and that these are formed from the contents of single large vegetative cells. The lack of flagellated reproductive cells was used by some phycologists to make a new genus (*Aegagropila* Keutzing 1849), but this condition no longer exists, since biflagellated swarmers have now been found in *Aegagropila* (Smith 1950). Pascher (1921) does not use reproductive means for key characters between *Cladophora* and *Aegagropila*, but separates them on the basis of the former being attached with a primary rhizoid, or in strands or wads without a primary rhizoid, and the latter being without primary rhizoids, forming a turf or cushion on the bottom, or free-swimming on the surface in ball form. As can be seen in the algal material, these distinctions are rather indefinite.

The following data, on the balls found, and on the area, may be of interest. Cayuta Lake is of glacial origin. It is approximately two miles long by one-half mile wide, and averages between four and six meters in depth, with a probable maximum of twelve to fifteen meters. It lies in a depression at an elevation of 1272 ft. and is surrounded by rather steep hills going up to 1850 ft. The following miscellaneous water data from Limnology class records were given the writer by Dr. C. O. Berg, professor of Limnology at Cornell University:

Date	Temperature (°F)	pH	Methyl Orange (p.p.m.)	Oxygen (p.p.m.)	Transparency (feet)
April 28, 1950	49	7.5	40	11.5	4.4
May 9, 1951	56	8.2	46	8.4	....
October 9, 1953	56	8.0	55	9.5	4.5

The bottom of the lake where the balls were found was of a swampy nature, with the balls in the lake proper, and intermingled with much sawdust from a sawmill formerly located above the lake. The balls *pave* the lake floor, and wash up on shore in windy weather (fig. 1). On bright, sunny spring days, gasses produced by the plants float the balls, and these also are washed onto the shore.

The filaments of the alga measured 65.7μ wide on the average, ranging from 34μ to 120μ, while the average cell length was 350μ. The average diameter of 50 balls gathered was 4.8 cm, with a range from 3.0 to 8.1 cm; this average, of course, was not general since it was of a selected sample, and the true range of sizes was from 0.5 to 10 cm. No reproductive processes have been observed either in the fresh material or in the laboratory material.

Since *Cladophora* balls have been reported in the literature only three or four times in the United States, it was thought desirable that their presence in Cayuta Lake, New York, be published. The present writer would be happy to hear of the presence of these unusual forms elsewhere in the country.—JESSE F. CLOVIS, University of Connecticut, Storrs, Conn.

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Notes on Arabis[1]

Arabis albida Stev.—Occasionally cultivated and apparently susceptible of establishing itself in Quebec. QUEBEC, KAMOURASKA: *Hamel & Payette* 7, Notre-Dame-du-Portage rivage à l'est du village, cordon de déchets au-dessus de la marée, une grosse touffe, 31 mai 1949 (DAO).

Arabis divaricarpa A. Nelson var. **dacotica** (Greene) stat. n., *Arabis dacotica* Greene, Leafl. Bot. Obs. Crit. 2:80 1910; *Arabis divaricarpa* A. Nelson var. *pinetorum* sensu B. Boivin, Can. Field-Nat. 65:16. 1951, nec *Arabis pinetorum* Tid., Proc. Biol. Soc. Wash. 36:182. 1923.

Leafing through the type collection at the Smithsonian Institution, I concluded that the common western Canadian phase of *Arabis divaricarpa* belongs with *A. dacotica* Greene rather than with *A. pinetorum* Tid. as previously stated. The latter has the pendant siliques, the reflexed pedicels, the pubescence, etc., characteristic of the species of the *A. holboellii* Horn. group.

The typical form, var. *divaricarpa*, has the siliques straight, neatly parallel and regularly ascending at a 45° angle. On the other hand, var. *dacotica* has the siliques frequently slightly falcate, more or less spreading to slightly ascending or descending at a variety of angles on the same plant thus giving to the inflorescence a rather untidy appearance.

Arabis divaricarpa A. Nelson var. **hemicylindrica** var. n.

Inflorescentia modo secunda, hemicylindrica, siliquis omnibus vel fere omnibus in 180° sparsis. Ceteris ut var. *dacotica*.

QUEBEC, GASPE: *Victorin & Germain* 49 422, Cap des Rosiers, éboulis calcaires, 20 juillet, 1937 (DAO).

SASKATCHEWAN, ASSINIBOIA: *Boivin & Dore*, 7992, Estevan, cliff bordering the valley of the Souris River, July 17, 1951 (DAO); KINDERSLEY: *Boivin & Alex* 9771, Gorefield, 7 milles au sud, écorre de la coulée Agassiz, inflorescence quelque peu seconde, 11 juillet 1952 (DAO). MAPLE CREEK: *Boivin & Alex* 9738, Carmichael, 10 milles au sud, monts Cyprès, écorre de la coulée du ruisseau Bone, inflorescence seconde ou parfois distique, 9 juillet 1952 (DAO type); *A. J. Breitung* 4401, Cypress Hills Park, open plateau, occasional, July 7, 1947 (DAO); MELVILLE: *Boivin & Dore* 7679, Agassiz coulée north of Rocanville, dry south-facing slope, more or less secund, July 6, 1951 (DAO); SWIFT CURRENT: *A. J. Breitung* 4088, Swift Current, riverbank, occasional, June 25, 1947 (DAO); *Boivin & Alex* 9698, Swift Current, 4 milles au sud, écorre du ruisseau Swift Current, inflorescence presque seconde, 8 juillet 1952 (DAO); WEYBURN: *Boivin & Dore* 7949, south of Macoun, dry south-facing embankment of the valley of the Souris River, July 16, 1951 (DAO); WOOD MOUNTAIN: *Boivin & Gillett* 8736, flanc nord du côteau Boisé au sud de la coulée Hudson à la hauteur du lac Bulkin (Bengough), alt. ca 775 m, zone à *Festuca scabrella*, 10 août 1951 (DAO).

ALBERTA, LETHBRIDGE: *Boivin & Alex* 9512, Milk River Ridge, 10 milles au sud-ouest de Milk River, vallée latérale d'une coulée glaciaire, siliques secondes, 26 juin, 1952 (DAO); MEDICINE HAT: *Boivin & Alex* 9539, Manyberries, 20 milles au sud, canton 2, rangée 5, écorre érodé bordant le Lost River Canyon, inflorescence seconde, 28 juin 1952 (DAO).

NORTH DAKOTA, WARD: *Boivin & Dore* 8063, east of Bowbells, Rivière-des-Lacs, dry hillside bordering the lake, July 19, 1951 (DAO).

When first encountered, this variety was considered to be the result of wind action permanently deflecting the inflorescence to one side. However, it was soon noticed that in any colony the inflorescences were not all facing in the same direction as would be expected if strong winds were to be the cause of these secund inflorescences. Therefore this variety is now presumed to be of genetic origin.

The varietal characteristic is not so obvious in the herbarium as in the field. The inflorescence of fresh specimens is more or less flat on one side, hemicylindric on the other, the siliques being distributed in an angle of ± 180°. Upon pressing, the siliques are all brought into the same plane and usually the secund nature of the inflorescence becomes

[1]Contribution No. 1469, Division of Botany and Plant Pathology, Science Service, Canada Department of Agriculture, Ottawa, Ontario.

hard to detect unless the specimen was pressed sideways, which on the other hand, also deforms the inflorescence by accentuating its secund nature. However, specimens that were not pressed sideways can still be recognized if they are fairly heavily fruited. Upon pressing, some of the siliques will come to rest upon or across the rachis of the inflorescence. These siliques will be all or nearly all on the same side of the rachis in var. *hemicylindrica*, while in var. *dacotica* there will be about as many on one side of the rachis as there are on the other.

Var. *hemicylindrica* is the common phase of this species along the coulees of the Johnston network, especially on the Alberta side. East of the Coteau, the variety also extends sporadically along the Agassiz and Souris coulees. In North Dakota it is found along the Rivière-des-Lacs coulee, a coulee parallel to the Souris. Presumably it will also be found in Montana, at least north of the Missouri.

Arabis divaricarpa A. Nelson var. *stenocarpa* Hopkins. Range extension and new to Manitoba. MANITOBA. BRANDON: *G. Stevenson* 410, Brandon, dry hillside, pasture, May 26, 1951 (DAO).

This variety is of doubtful status and may represent nothing but an extreme of variation. However its known distribution is still incomplete and it is not yet possible to decide whether it is just a random variation or a geographical variety in its own right. Known localities are Bic, Brandon, Pilot Butte, Mortlach and Prince Albert. This distribution suggests that the variety might have formerly been extensively distributed on bluffs bordering the periglacial lakes and the Champlain sea but is now barely persisting in a few widely scattered localities.

Arabis retrofracta Graham var. *collinsii* (Fern.) B. Boivin. Common from Manitoba westward and long known in the east at Bic as a postglacial prairie relic, this plant has also been found half way between Bic and Manitoba. QUEBEC. PONTIAC: *Bassett & Mulligan* 1172, Power Station, Calumet Township, shallow sandy soil over marble rock, only 3 plants seen, June 17, 1950 (DAO). *G. Lamarre* 45-75, Waltham, sur les rochers le long de la grande route, 5 juin 1945 (DAO).—BERNARD BOIVIN, Botany and Plant Pathology Division, Ottawa, Ontario.

Additional South Dakota Terrestrial Gastropod Records

A small collection of terrestrial pulmonates from Pennington and Custer counties, South Dakota, was recently transmitted to me through the kindness of the collectors, Dr. and Mrs. Herbert Levi, of the Department of Zoology, University of Wisconsin. These specimens, now deposited in the University of Utah collection, materially supplement my attempt to summarize the published records from South Dakota (Roscoe, 1954, Table 1). In the list below new county records are indicated by an asterisk.

Near Game Lodge, Custer Co. June 19, 1951.—**Discus cronkhitei* (Newcomb).

Three miles east of Pringle, Beaver Creek Spring, in dry meadow, Custer Co. August 7, 1954.—*Vallonia gracilicosta* Reinhardt.

Harney National Forest, near Jewel Cave, Custer Co., June 29, 1952.—**Discus cronkhitei* (Newcomb); **Euconulus fulvus alaskensis* (Pilsbry); **Pupilla blandi* Morse; **Succinea avara* (Say); **Vertigo concinnula* Cockerell; **Vitrina alaskana* Dall; **Zonitoides arboreus* (Say).

Horsethief Lake, under lumber, Pennington Co. June 21, 1952.—*Discus cronkhitei* (Newcomb); **Euconulus fulvus alaskensis* (Pilsbry); *Retinella electrina* (Gould); *Vallonia gracilicosta* Reinhardt; **Vertigo concinnula Cockerell*; **Zonitoides arboreus* (Say).

I take this opportunity to append here several records contained in Pilsbry's Monograph of the Land Mollusca of North America (1939-48) which were inadvertently omitted from my previous paper. The tranquility of my conscience will, in some measure, be restored by this rectification.

Forms to be added to Table 1 (Roscoe, 1954): *Discus cronkhitei catskillensis.*—Remington Co.; *Helicodiscus eigenmanni arizonensis.*—Clay, Lincoln, and Deuel Cos.; *Vallonia albula.*—Lawrence Co.

Additional county records for forms recorded in Table 1 (Roscoe, 1954): *Anguispira alternata.*—Clay Co.; *Carychium exile.*—Lincoln Co.; *Discus cronkhitei.*—Lincoln Co., Carson Co. (drift); *Gastrocopta procera.*—Washington Co.; *Helicodiscus parallelus.*—Carson Co.; *Helicodiscus singleyanus.*—Lincoln Co.; *Punctum californicum.*—Lincoln Co.; *Succinea grosvenori.*—Vermillion Co.. *Vallonia parvula.*—Lincoln Co.; *Vallonia perspectiva.*—Brule Co.

Published records lacking specific county designations were disregarded in the preparation of my previous paper. This procedure resulted in the omission of the following two gastropods cited at this time for the benefit of those desiring to have a complete list of the land snails known to occur in South Dakota: *Gastrocopta pentodon* Say; *Deroceras laeve* (Müller).

Unfortunately a number of typographical errors are present in the "Literature Cited" section of my 1954 paper. Rather than attempt to correct these seriatim, I reproduce below a corrected bibliography of the South Dakota terrestrial gastropod literature.—ERNEST J. ROSCOE, University of Michigan, Ann Arbor.

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